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THE JOURNAL  
OF  
Comparative Neurology

A QUARTERLY PERIODICAL  
DEVOTED TO THE  
Comparative Study of the Nervous System.

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## THE STRUCTURE AND MORPHOLOGY OF THE OBLONGATA IN FISHES.

By B. F. KINGSBURY.

*With Plates I-V.*

The writer was engaged in the study of the Amphibian brain at the time of the appearance of the monograph by O. S. Strong on the cranial nerves of Amphibia. Especially was it then attempted to determine in *Necturus* the ental origin of the nerves of the oblongata, and many results attained by Strong had been independently gained by me, largely under the stimulus of his preliminary papers, but the broad view and general application which made Strong's paper so valuable a contribution were in a degree wanting in my own.

In Strong's comparison of the cranial nerves of Amphibia with those of "fishes" in the effort to find in the latter the representatives of the components already recognized by him, it was difficult to harmonize the accounts by various writers of the origin of certain of the nerves in the different forms. When, therefore, opportunity was afforded me during the past year of studying the brains of several ganoids and teleosts, especially *Amia* and *Aminurus*, one of the objects was to confirm the homologies suggested by Strong, to find in these forms the representatives of the nerve components previously recognized in Amphibia, and to identify in these so variously modified brains the corresponding regions, and determine their morphologic and structural relations.

It is the ultimate purpose, as just suggested, to work out somewhat carefully by means of the Weigert and Golgi methods the structure and relations of the regions of this part of the brain for certain ganoids and teleosts, in order to gain a more exact knowledge of the connections of the various nuclei with each other and with the rest of the brain and myel. This



last task is far from complete; however, pending the time when results in this difficult field may be gained of sufficient definiteness and coherence to render their publication of value, a more general consideration of the dorsal portions of the oblongata in fishes may serve to emphasize the regions whose various modifications have produced the truly enormous structures of certain teleosts, namely;—(1) the center of the acoustic and lateral line system nerves; (2) that portion which is the undoubted representative of the *fasciculus communis* portion of the Amphibian oblongata; and (3) the spinal fifth tract, the direct continuation of the dorsal columns of the myel. These are three *systems* having constant relations to certain cranial nerves, and should have names indicative of their character. It seems unwise, however, to introduce new terms. They will be spoken of as the ( *Systema* ) *acusticum*, the *fasciculus communis* or ( *fasciculus* ) *communis* system and the spinal Vth ( fifth ) tract, respectively.

The forms considered here<sup>1</sup> comprise 17 species, representing among the teleosts 10 families and 5 orders. Although far too few to permit any general conclusions being safely drawn as to the characteristic development in the various orders or even families, they yet strongly suggest what may be the case, and have given a far better idea of the extent and significance of the modifications of the regions.

This study was conducted by means of serial sections made through this region of the brain. Where but a single series was made the sections were transverse; in some cases supplementary series were made in the other two planes. The brains were fixed in Fish's picro-aceto-sublimate (formula: picric acid, 1 gram; mercuric chloride, 5 grams; glacial acetic acid, 10 c.c.; 50% alcohol, 1000 c.c.) or vom Rath's picric-sublimate-acetic mixture (formula: picric acid, sat. aq. sol. 100 c.c., hot sat. sol. mercuric chloride 100 c.c., glacial acetic acid. 2 c.c.).

<sup>1</sup> Namely, *Amia calva*, *Lepidosteus osseus*, *Acipenser rubicundus*, *Amiurus nebulosus*, *Catostomus teres*, *Notemigonus chryssoleucus*, *Exoglossum maxillilingua*, *Notropis cornutus*, *Cyprinus carpio*, *Clupea pseudoharengae*, *Esox reticulatus*, *Cottus ichtalops*, *Perca flavescens*, *Lepomis gibbosus*, *Roccus chrysops*, *Fundulus diaphanus*.

Of these two the aqueous formula seemed more satisfactory, although they were not tested for comparative results. With these the stains employed were Delafield's hematoxylin and Van Gieson's picro-fuchsin. The hematoxylin and picro-fuchsin were preferably used separately and all staining was in section. The hematoxylin was used much dilute and allowed to act some time and overstain slightly; subsequent staining in the picro-fuchsin lasted until all the hematoxylin was removed from the collodion in which all the brains were embedded and cut. An alcoholic (67 %) picro-fuchsin stain was also employed. Weigert staining was conducted in the usual manner and these brains were fixed and hardened in 3 and 5 % solutions of potassium dichromate several weeks.

The work was conducted in the Anatomical laboratory of Cornell University, and to the Anatomical Department I am indebted for much material and all the facilities of research. Professors Wilder and Gage have helped me with their kindly interest, suggestions and advice, and the latter has lent me personal assistance in procuring material; for all of which I would express my grateful appreciation. All the *Acipenser* material was obtained and fixed by Dr. O. D. Humphrey of Erie, Pa., and to his care and skill the results obtained were due.

Of the forms studied, the Ganoids, and *Amia* in particular, form from every point of view the more natural and convenient basis for comparison and point of departure in studying the oblongata of bony fishes. Because of the presence of a cerebellum of typical structure, and the even development of the parts of the oblongata, *Amia* presents advantages over the simpler urodelan brain on the one hand and the other ganoids (as far as studied) and the teleosts on the other, which present greater though different complexities. Therefore it will be advantageous to discuss somewhat the oblongata and cranial nerves of *Amia*; avoiding, however, all details not necessary in connection with the purpose of this paper.

The transition from myel to oblongata in *Amia* is gradual enough, and the cornua of the cinerea well enough defined (as contrasted with the simpler *Necturus*) to permit the following of



myelic structures into the oblongata, and it is in the dorsal portions, as usual, that the change is most marked. In a section of typical myel the ventral cornua are narrow and extend latero-ventrad; dorsad of the myelocoele is a region of cinerea from which the delicate dorsal cornua extend terminating in swellings composed of amyelinic fibers and "ground substance" with numerous small cells interspersed. Surrounding these on the dorsal, mesal and lateral sides are fine closely aggregated myelinic fibers. The ventral tracts are composed of coarser fibers with the characteristic Mauthner fibers; the lateral tracts are formed of fibers, in general, intermediate in caliber between those of the dorsal and ventral portions.

As the oblongata is approached, the dorsal horns enlarge, gaining a size three or four times that characteristic of the myelic portion (Figs. 6 and 13). At the same time the typically small myelocoele enlarges and assumes a subtriangular section; the sulci forming the angle extending toward the dorso-meson and the ventral cornua. The larger part of the dorsal fibers disappear and just caudad of the metatela a concentration of fine fibers on the dorso- and ventro-lateral sides of the cornua mark the first recognizable appearance of the spinal Vth tract. At this level the dorsal cornu and the gelatinosa rapidly disappear. (Fig. 15).

Near the caudal end of the metatela, a lateral sulcus appears, and dorsad of it the first appearance, as such, of the fasciculus communis (lobus vagi). (Fig. 15).

Increase in size of the fasciculus communis tract and migration ventrad of the spinal Vth tract give the former for a short distance a dorsal position. Soon, however, there appears dorsad of the spinal Vth tract and the fasciculus communis an area of fibers and intermingled small cells, which increases rapidly in extent and soon becomes capped by a layer of amyelinic substance, the cerebellar crest (cerebellarleiste of Goronowitsch), a caudal continuation of the molecular layer of the cerebellum (Figs. 16, 17). The change in the morphology of the oblongata from this point cephalad is simply in the increase in size of this, the acusticum, displacing farther ventrad the spinal Vth

tract, and the revolution of the wall between the ventral and lateral sulci somewhat from a vertical to a more horizontal position (Figs. 16-18).

*Nerves.* The vagus nerve arises by 4 (or 5) large roots each made up of two or three smaller rootlets. The most caudal root is undoubtedly purely motor and may be recognized some distance caudad of the metatela as an ascending tract.<sup>1</sup> As it passes cephalad it is reinforced several times by fibers from the the ventral horn, especially at its exit where a number of fibers come from the motor vagal nidus (Zwischenzellen of Goronowitsch) now recognized as a distinct cluster of cells. (Fig. 15, ni). The roots cephalad contain both motor and sensory (ganglionated) fibers and all arise in much the same way, the sensory from the fasciculus communis system (lobus vagi) as shown in Fig. 16, the motor from the vagal motor nidus and apparently also from cells of the ventral cornu proper, though they may yet arise from cells of the vagal nidus, the neurite simply bending ventrad first, it having in no case been traced into any cell. The caudal rootlets go ventrad of the spinal Vth tract, the cephalic ones dorsad of it (Fig. 16), while the intermediate roots break through it in passing to their exit. It was difficult to determine definitely whether the vagal roots which penetrated the spinal Vth tract drew fibers from it or not. However, those which passed dorsad to it clearly received a small contingent of fine fibers from it. This is important. Strong, from the fact that in Amphibia vagal fibers were closely associated with the spinal (ascending) Vth, considered it probable that the same source for a portion of the fibers of the Xth existed in other Ichthyopsida. It will be seen later that a similar derivation of a portion of the fibers of the Xth occurs in at least some teleosts.

Accompanying the vagus is the lateral line nerve which after the former enters the brain continues cephalad some distance and is joined by the IXth which reaches it after piercing

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<sup>1</sup>In this respect there is a close resemblance between *Amia* and *Necturus* (Amphibia).



the ear-capsule. The lateral line nerve is composed of the characteristic fibers with dense sheaths. It also receives a small contingent of fine fibers from the IXth and in turn gives to it a small bundle of its coarse fibers.<sup>1</sup> The IXth enters the brain first (Fig. 17) and sends a bundle to the fasciculus communis and one to the lateral nidus of cells, a continuation of the vagal motor nidus. The lateral line nerve soon enters the dorsal tract, the acusticum, just ventrad of the cerebellar crest and the fibers can be traced cephalad for some distance; whether any of them enter the cerebellum or not as Goronowitsch found in *Acipenser* has not been satisfactorily determined; it seems improbable.

Ascending fibers of the VIIIth nerve may be recognized at the level of the IXth, dorsad of the spinal Vth. This nerve leaves the oblongata just dorsad of the spinal Vth tract. Other fibers of the VIIIth seem to terminate immediately on entering the brain near the characteristic large laterally situated cells, so regularly found, and a few turn cephalad; however, the relations in this complicated region have not been made out at all satisfactorily as yet. So far, *Amia* agrees quite closely with *Acipenser*, but in the origin of the remaining roots near the VIIIth there is a considerable difference. In the first place there does not exist in *Amia* the dorsal prominence present in *Acipenser* which was termed by Goronowitsch "lobus trigemini," and the nerve root issuing therefrom (*Trig. II dors.* of Goronowitsch) is absent as such. Very close to the VIIIth, so close as to be indistinguishable from it macroscopically, there arise in dorso-cephalic succession, VIIb and VIIaa;<sup>2</sup> the former of coarse

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<sup>1</sup>Allis described the innervation of a dorsal line of free neuromasts and a canal organ by fibers of the IXth nerve. Undoubtedly the fibers received from the lateral line nerve have this distribution. It is precisely what we should expect.

<sup>2</sup>The names by which the roots were designated by Strong in Amphibia are here used to indicate the homologous roots in fishes. The reference of VIIb and VIIaa to the VIIth nerve are matters of convenience merely; VIIaa, seems, however, the undoubted homologue of the "pars intermedia Weisbergii."

The designation of the other cranial nerves by numerals is adhered to as better facilitating reference. It is insignificant otherwise.

fibers identical in appearance with those of the lateral line nerve and entering the acusticum, and the latter from the fasciculus communis system which disappears with the exit of this root. (Fig. 18). Cephalad of the VIIIth is the motor VIIth (VIIab) which has the typical mode of ental origin so constant in vertebrates and so well described in *Acipenser* by Goronowitsch. In addition to these there arises, sometimes ventro-cephalad of the VIIIth, sometimes dorsad,—there being a variation in this respect apparently,—a root composed of fibers from the spinal Vth. When it arises ventrally the fibers are drawn directly from the spinal Vth tract; when farther dorsad the fibers which form it have a course upon the ectal surface of the acusticum, from which the bundle may be easily distinguished, and may be traced caudad as a distinct strand as far as the cephalic rootlets of the Xth where it joins the spinal Vth proper. To which nerves (rami) these fibers eventually go has not been determined.

Some distance cephalad the remainder of the spinal Vth leaves the brain in connection with two rootlets from the trigeminal motor nidus to constitute the Vth nerve proper. A mesencephalic component was not recognized although the characteristic cells of the roof were found, and doubtless a root exists although I have not been able to determine its presence. So much as has been said of the cranial nerves in *Amia*, while not sufficient for a consideration of the nerves themselves will permit the recognition of the components recognized by Strong, and may serve to introduce a discussion of the corresponding regions of the oblongata, namely, as before mentioned, the spinal Vth tract, the fasciculus communis system, and the acustic system, the acusticum. A more minute discussion of the origin of the nerves and the structure of the oblongata is reserved.

*Spinal Vth tract.* The existence of the spinal (ascending) root for the trigeminal nerve has been quite generally recognized throughout the vertebrate branch and needs no comment here. Among Ganoids in *Acipenser* only had the presence of "ascending" trigeminal fibers been recognized, by Gorono-



witsch, though they were not followed caudad any distance. The view also that this tract represents the dorsal column in the myel and that its fibers correspond to the sensory fibers of spinal nerves needs not be emphasized. In fishes, teleosts especially, the correctness of this view seems quite evident and has been recognized by Mayser. In higher vertebrates we find this view supported by Kölliker, Gaskell and Turner; the latter considers the spinal root of the fifth and the solitary tract homodynamous, and apparently considers that both together represent the dorsal columns; Minot regards the *tractus solitarius* as continuing in the oblongata the dorsal column of the myel (*fasciculus ovalis* of the embryo). It is impossible therefore to draw any entirely satisfactory conclusions as to the representative of the dorsal column in the oblongata, since facts of development in all but mammals are wanting. The homology of the vagal component derived from this system in some lower forms, and of the *tractus solitarius*, is involved. Strong considers the *fasciculus communis* as the homologue of the *tractus solitarius*. Minot states that the late development of the spinal Vth tract in man interferes with a true comprehension of its value.

In *Amia* (and in certain teleosts at least) not only does this system furnish fibers for the Vth, but also for the Xth, as Strong assumed would be the case. The exit in *Amia* of a small portion of the fibers with the VII-VIII appears to be an exceptional condition, though constant in the few brains examined for it. An important point in regard to this tract in *Amia* (and other Ganoids) is that it is superficial. The enlargement of the dorsal horns caudad of the metatela produces corresponding ectal swellings resembling the clavas of the mammalian brain, and from these in specimens in which all connective tissue has been removed from the surface of the oblongata, the spinal Vth can be traced. A slight swelling caused by the tract and a difference in color from the surrounding portions, due apparently to the concentration of the fibers, renders it easily distinguishable with the unaided eye. It seems especially prominent in formalin preparations, and can be followed

readily into the Vth nerve (Fig. 3). Likewise in *Lepidosteus* the same tract may be macroscopically recognized.

*Fasciculus communis* system. It afforded considerable pleasure to recognize how exactly homologous the *lobus vagi* of Ganoids<sup>1</sup> is with the *fasciculus communis* of the Amphibian brain, thus confirming the homology proposed by Strong. In Teleosts, however, the homology should also be extended to the lobus trigemini, when that structure exists. In certain Teleosts (Nematognathi and Eventognathi as far as examined) the portion of the fasciculus communis system associated with the pre-auditory root (VII aa) is considerably developed and even (Eventognathi) fuses with its fellow across the meson (*Tuberculum impar*). This it is which was termed by Mayser *lobus trigemini*. The following table sets forth homologies the correctness of which will better appear later.

	<i>Postauditory</i>	<i>Preauditory</i>
Amphibia.	Fasciculus communis	Fasciculus communis
Ganoids.	Lobus vagi	Lobus vagi
Elasmobranchs	Lobi vagi	Lobi vagi (?)
Teleosts (some)	Lobus vagi	Lobus trigemini

The name *fasciculus communis* first given by Osborn to this structure of the Amphibian brain has been adopted by Strong, Burckhardt and the writer, for Amphibia and more generally applied (in *Amia*) by Allis, and seems to have become firmly established. It is unfortunate that the study proceeded from the Amphibia to fishes instead of in the reverse direction, since when the term fasciculus is applied to other Ichthyopsida it becomes somewhat inappropriate. Therefore some hesitation was felt in employing the name here. It should be remembered that it is not a fasciculus but a system or region of the oblongata. In those teleosts in which there is a distinction between

<sup>1</sup> The old term Ganoids is employed as a matter of convenience merely and is not intended as a prejudgement of the question of recognizing them as a distinct group. There are however some differences in the nervous system in Ganoids and Teleosts which I believe will prove to be constant.



the pre- and the post-auditory portions of this system the old terms *lobus trigemini* and *lobus vagi* are retained, the fact being recognized, of course, that the nerve root from the former belongs rather (on the present nomenclature) to the VIIth than to the Vth nerve. The "*lobus trigemini*" of Elasmobranchs and sturgeons will be referred to later.

Even in its highest development in Amphibia the *fasciculus communis* is much simpler than in Ganoids and appears simply as a highway in which fibers of a constant and peculiar appearance turn caudad from the VII, IX and Xth nerves; and the cells of the adjacent cinerea sending processes into the tract must be considered with it as the end nidus. The so-called *lobus vagi* of Ganoids includes nerve cells and thus must be more than the fasciculus communis of Amphibia. This tract in *Amia* resembles closely that in *Acipenser* and the description of Goronowitsch applies to *Amia* as well. The tract first appears near the caudal end of the metatela, just beneath the endyma. It increases rapidly in size and soon produces a marked swelling in the wall of the oblongata, occupying the most dorsal region, from which it is soon displaced by the development of the *acusticum* (dorso-lateral tracts) (Figs. 15-17). From it arise by far the greater part of the sensory fibers of the Xth and IXth nerves and a large root of the VIIth with the exit of which it disappears. In structure it consists of fine fibers with areas of ground substance and interspersed small cells, which also form a layer just beneath the endyma. The general resemblance between this structure in Ganoids and in Elasmobranchs is quite close.

*The Acusticum.* The most dorsal portion of the oblongata in *Amia* is occupied by the "dorso-lateral" tracts, which constitute the centre for the acustic and nerves of the lateral line system, and is here spoken of as the acusticum. It has certain constant connections with the rest of the brain and is capped by a caudal extension of the molecular layer of the cerebellum (cerebellar crest) as already stated. This intimate association of cerebellar structure with this portion of the metencephal is very striking and suggestive. Roughly speaking, in mammals

and birds the cerebellum consists of a cortex of well defined and characteristic structure and an ental mass of fibers. In reptiles the last seems to be wanting or ill-defined and the granular layer of the cinerea (cortex) becomes more closely applied to the endyma. Among the Ichthyopsida the simplest condition of the cerebellum exists in Urodeles, *Petromyzon* (Marsipobranchs?) and *Protopterus* (Dipnoans?) where it is represented by a bridge over the cavity cephalad of the metatela, composed of fibers passing from one side to the other, and an associated and sometimes insignificant layer of apparently indifferent nerve cells. In presumably all the remaining classes, at least in Ganoids, Teleosts and Elasmobranchs (*Rohon* '77, *Viault* '76, *Sanders* '86) the cerebellum presents the structure typical of the cerebellar cortex in higher forms, namely, an ental granular mass or layer and an ectal molecular layer of fine fibers, and between them a more or less well defined zone of large cells sending their dendrites into the molecular layer,—undoubted Purkinje cells. In all these (as far as examined) the molecular layer extends caudad over the oblongata, and in *Ganoids and Teleosts so far as investigated, it is associated only with the portion serving as the center for the acoustic and lateral line system of nerves, the Acusticum*. This is an important relation that should be emphasized. In some forms at least, (e.g. *Amiurus* et. al. Fig. 11.) the layer of Purkinje cells also extends caudad upon the oblongata. In sharks and rays the molecular layer extends almost to the caudal limit of the metatela covering in part the so-called Lobi trigemini<sup>1</sup> and the *corpora restiformia* which also possess the granular and Purkinje cell layers.

Ascertainment of its exact relations in the oblongata of

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<sup>1</sup> "Im innigen Zusammenhange mit den *Lobi trigemini* stehen auch die *Corpora restiformia* welche gleichfalls nur eine directe Fortsetzung der oberen durcheinander gewundenen Hinterhirnsubstanz vorstellen. Anfangs bestehen die *Corpora restiformia* aus der Grundsubstanz oder Neuroglia [molecular layer] und den Antheilen der inneren Hinterhirnmassen, später aber bleibt von ihnen nur die Neuroglia zurück, welche sich als ein Mantel auf den oberen Seitenmassen des Nachhirnes, die Pedunculi cerebelli bedeckend, bis in die Hinterstränge des Rückenmarks erstreckt, wo sie die Substantia gelatinosa Rolando zum grössten Theile darstellt." *Rohon*, p. 84.



Elasmobranchs may render easier a close homologization of the regions there. So impressed was Goronowitsch with this relation of the molecular layer of the cerebellum in *Acipenser* that he regarded it as an indication of the primitive integrity of cerebellar and oblongatal regions.<sup>1</sup> Whatever may have been the primitive morphologic relations of the cerebellum to the oblongata, the point that should be emphasized, it is felt, is rather the present physiologic relation which must exist between the cerebellum and that,—morphologically most dorsal—part of the oblongata serving as the centre for the nerves of the ear and lateral line organs. Schaper has found that in teleosts as in mammals the fibers of the molecular layer arise by a forking, T-shaped origin of the neurites of the cells of the granular layer. In *Amia* and many if not all teleosts a large part at least of the fibers of the cerebellar crests of the two sides decussate in the caudal wall of the cerebellum, most clearly seen in *Amiurus*. This and other evident connections may better be discussed subsequently.

At this point very brief mention may be most conveniently made of *Lepidosteus* and *Acipenser*. A single specimen of the former was available. The resemblance between the oblongata of *Amia* and *Lepidosteus* is very close. As in the former, there is no trace of the so-called *lobus trigemini* of *Acipenser* nor any root to correspond to *Trig. II dors.* of Goronowitsch. The nerves present in *Amia* and their components were easily recognized, except that, since no Weigert preparations could be made, it was impossible to determine satisfactorily the relations of the spinal Vth tract; however, it is undoubtedly superficial and much as in *Amia*.

The peculiar interest attaching to *Acipenser* (or other stur-

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<sup>1</sup>“Die innige Verbindung, welche zwischen Cerebellum und Medulla oblongata bei primitiven Formen nachzuweisen ist, berechtigt die Vermuthung, dass wir es hier mit einem primitiven Character zu thun haben. Es erscheint demnach denkbar, dass das streng von der Oblongata differenzirte Cerebellum der höheren Wirbelthiere durch allmähliche Reduktion der Cerebelargebilde der Oblongata und durch eine allmähliche Koncentration dieser Gebilde im differenzirten Hinterhirne der höheren Wirbelthiere entstehen konnte.” etc. Goronowitsch, p. 539.

geons) led me to examine the oblongata and especially the "lobus trigemini." As described by Goronowitsch there occurs dorsad of the cerebellar crest in the region of the VIIIth nerve and extending cephalad, an area of cells and fibers from which springs a nerve root (his *Trigeminus II dorsalis*). Immediately beneath the cerebellar crest issues another root of coarse fibers, clearly VIIb of *Amia*. The fibers of the dorsal root are indeed finer than those of the more ventral, but the difference is not nearly as marked as one might suppose, and as compared with the fibers of VIIaa, they are coarse. *Trig. I ventralis* of Goronowitsch was found upon examination to spring, in several rootlets from a motor nidus and not from the posterior longitudinal fasciculus, representing the motor portion of the Vth in *Amia*. The tract named by Goronowitsch "system  $\gamma$ " is clearly both from the description and the examination of the brain, what was found in *Amia* to be part of the spinal Vth tract, and from the examination of *Acipenser* the same seems to be the real destination of this tract there. System  $\gamma$  would not in any case be more than a partial homologue of the secondary vago-trigeminal tract of the teleostean brain. The fact remains, that *Acipenser* possesses a root of comparatively coarse fibers, which is not present in *Amia* and *Lepidosteus*, springing from a portion of the brain which is also apparently lacking in these two forms. This the "lobus trigemini" will prove, I believe, to be the homologue of the structure of the same name in Elasmobranchs.

*Teleostei.* As compact a discussion as possible of these regions and their modifications in teleosts follows.

*Nematognathi.* In view of the belief of some that the Nematognathi among teleosts are the most closely related to Ganoids, we might expect *Amiurus* to show in the structure and morphology of its brain, some indications of ganoid affinities, but as has been already stated by C. J. Herrick '91, it presents as purely teleostean characters of the brain as other bony fishes, although simpler in some respects than many,—perhaps most,—other Teleosts. The morphology of the oblongata and the more striking and important structural features have been pre-



viously discussed by Wright and need only be referred to in so far as they affect the dorsal region. Except for the teleostean characteristic of greater concentration of fiber tracts into distinct bundles, the oblongata of *Amiurus* would be directly derivable from the ganoid type as presented in *Amia* by a concentration of structure and a great development of the fasciculus communis system, especially the preauditory portion of its root, and the limitation of the acusticum to the dorsal side. To harmonize the relations here with those in other forms and illustrate points already made, the following may be noted.

The enormous enlargement of the dorsal cornua of the myel as the oblongata is approached, is a condition apparently quite universally present in "fishes;" in *Amiurus* the changes closely compare with those in Cyprinoids as described by Mayser. Figures 7-10 will give an idea of how clearly the relation of parts is indicated in *Amiurus*. Caudad of the oblongata occurs the enlargement of the dorsal cornua; these, with the surrounding fibers move laterad and the fasciculus communis systems appear on the dorsal portion, the two sides connected caudad of the metatela by the *Commissura infima Halleri*. The dorsal cornua rapidly diminish and about them on the dorsal and lateral sides the fibers of the spinal Vth tracts appear,—pushed ventrad by the greatly developed fasciculus communis systems (lobi vagi) which now occupy the dorsal region of the oblongata. Cephalad of the Xth there appears at the side of the oblongata a new structure, which spreads ventrad covering ectally the spinal Vth tract and soon is capped on the dorsal side by the cerebellar crest. This is easily recognized as the homologue of the acusticum of *Amia*, the *tuberculum acusticum* of Wright. In *Amiurus* and indeed other teleosts, it is not purely dorsal but extends laterally over the oblongata, submerging the spinal Vth which until the appearance of the acusticum, was superficial. The pre- and postauditory portions of the fasciculus communis are differentiated into the so-called "trigeminal" and "vagal" lobes; the former are enormous and dove-tail into each other; they extend dorsad and displace the acusticums laterally (Figs. 5 and 11), but no fusion occurs,—at least not in the individuals

examined, although it may possibly be found in older specimens.

Of the cranial nerve roots little need be added to Wright's account. The sensory portion of the Xth springs from the lobus vagi in a single large root, passing dorsad of the spinal Vth. A small contingent of fibers from this tract was easily demonstrable. The motor portion of the vagus springs from its nidus just ventrad of the fasciculus communis in 8-10 small roots which pass on the ventral side of the spinal Vth. A root bundle of the Xth composed of coarse fibers of characteristic appearance, undoubtedly the lateral line nerve, passes cephalad from the Xth accompanied by a fine fibered bundle (IX) which enters the brain first, penetrating the acusticum to reach the fasciculus communis (Fig. 24), while the coarse fibered root enters the acusticum just ventrad of the cerebellar crest and may be traced cephalad some distance. From the lobus trigemini arises an enormous root, VIIaa, the "dorsal geniculate root of the Vth;" and close to it there arise, (1) from the acusticum dorsad of it a root which as Wright determined innervates the neuro-masts (VIIb), (2) caudad and ventrad, the VIII, and (3) the facial proper arising in its usual manner and leaving the brain ventrad at about the level of VIIaa. A slight distance cephalad there arises the Vth proper, composed of the spinal Vth and two bundles from the trigeminal motor nidus. No mesencephalic origin for any of the fibers has as yet been recognized in *Amiurus*.

It is not at all difficult to recognize here the same components present in *Amia*; most notable is the enormous development of VIIaa. It is to be noted also that in *Amiurus* there occur no fusions across the meson, such as are found in other teleosts, neither of the lobi trigemini nor the acusticums; what Wright described as a fusion of the latter is the decussation of the fibers of the cerebellar crest in the cerebellum. The massing of the fasciculus communis system and especially the development of the preauditory part as the lobus trigemini has displaced the acusticum from its typically dorsal position and crowded it to the side. By a reduction of the fasciculus communis element and a cephalo-caudal stretching of the oblongata,

especially of the acusticums, the form might be easily reduced to that of the following order.

*Haplomi.* In *Esox* and *Fundulus*, the two representatives of this order examined, the conditions are even somewhat more satisfactory than in *Amiurus*, since the communis system is much more weakly and evenly developed. The exact caudal limit of this system is in *Esox* somewhat difficult to determine exactly from the material at hand. A common mesal area representing the *comm. infima Halleri* appears between the dorsal cornua and is soon divided into the paired tracts at the caudal end of the metatela. The Xth arises by 4 or 5 closely associated roots which contain both sensory fibers from the fasciculus communis and motor from the vagal nidus (*ni*). These all pass ventrad of the spinal Vth. Cephalad of these the acusticum appears in transection dorsad of the spinal Vth, and is soon capped by the cerebellar crest. An isolated root (IX?) composed of communis and motor components enters, penetrating the acusticum, cephalad of which and near the entrance of the lateral line root another small root from the communis system and motor nidus enters. The lateral line nerve enters the acusticum immediately beneath the molecular layer. The VIII nerve springs from the acusticum by 2 (or 3) roots, dorsad and cephalad of which arises VIIb, followed by VIIaa and VIIab, the former at about the same level, the latter farther ventrad. The spinal Vth leaves the brain a short distance cephalad accompanied by motor strands (2 or 3) from the trigeminal motor nidi.

*Fundulus*, in the structure of its oblongata closely agrees with *Esox*; the caudal limit of the fasciculus communis systems was clearly defined and easily distinguished from the dorsal cornua. The Xth arises in 3 divisions, the sensory fibers (from the communis system) dorsad and the motor ventrad of the spinal Vth. Isolated sensory and motor roots (IX?) enter farther cephalad, the former from the fasciculus communis, the latter from a motor nidus. The lateral line nerve is small; its relations are as already described. VIII, VIIb and VIIaa leave the brain very near each other and the Vth follows closely.



In these two fish the fasciculus communis system is evenly developed. At the exit of the Xth it is dorsal but it is soon displaced by the acusticum. There is no "lobus trigemini"; VIIaa develops as the fasciculus communis diminishes and has a short cephalic course before leaving the brain. In *Fundulus* this root and also the entire communis system is somewhat better developed than in *Esox*. In *Esox* there is a division into two quite well defined regions. No vagal fibers were seen to spring from the spinal Vth. No Weigert preparations were made and on further study no doubt such a component will be found to exist. Important it is in view of the conditions in the forms to be mentioned, that in these, as in *Amiurus*, there are no secondary fusions of endymal surface in the oblongata (Fig. 20).

*Acanthopteri.* Four spiny-rayed teleosts were studied, representatives of as many families,—*Roccus*, *Perca*, *Cottus*, *Lepomis*. In these one important general difference from the forms hitherto mentioned occurs in the dorsal fusion of the acusticums across the meson (Fig. 19). It extends from about the region of entrance of the lateral line nerve cephalad nearly to the exit of the VIIth. It is substantial, involving the molecular layer and the portion beneath it, obliterating the endyma and giving passage to fibers from side to side. Aside from this the relative development of the regions of the oblongata is much as in the Haplomi. The communis system is but slightly developed and there is no differentiation of pre- and postauditory portions. A few words may be said in description of each separately.

In *Roccus*, (Fig. 23) the fasciculus communis system appears some distance caudad as a mesal area between the dorsal cornua. The development of the spinal Vth tract upon the dorsal and lateral sides of these and its direct continuity with the dorsal fibers of the myel are very clearly shown.

The Xth arises by 7-8 poorly defined roots which pass ventrad of the spinal Vth. It derives a distinct component of fibers from this tract. The lateral line nerve enters in the characteristic place just beneath the cerebellar crest, and at the same level a fine fibered root from the Xth which passes cephal-

ad in company with a portion of the VIII, enters, going dorsad of the spinal Vth to the fasciculus communis system. VIIaa is well developed and its deep course and origin are as in *Esox*. A slight endymal fusion occurs between the caudal portions of the fasciculus communis systems. It is insignificant.

In *Lepomis*, as in *Roccus*, the spinal Vth tract is very prominent on the surface of the dorsal cornua. The roots of the Xth pass ventrad of the tract and derive a component from it. The isolated cephalic vago-glossopharyngeal root enters just caudad of the lateral line nerve and near the beginning of the fusion.

In *Perca* (Figs. 12 and 19) also, the spinal Vth tract is strongly pronounced, the fibers being grouped in two bundles. The Xth nerve passes ventrad of it and receives a strong strand of fibers from its dorsal division (Fig. 12). The cephalic root enters as before described, dividing the spinal Vth tract in its passage to the fasciculus communis.

In *Cottus* no spinal Vth component to the Xth was recognized with certainty. The fusion of the acusticums was not as strong as in the other three forms.

In all the origin of VIIaa was as already described in *Esox*, having a cephalic course after its formation before leaving the brain. The fasciculus communis system was most developed in *Roccus* and *Lepomis*, where, as in *Esox*, there was an indication of two regions, dorsal and ventral.

*Isospondyli*. A single species belonging to this order was examined, the alewife, *Clupea pseudoharengae*, and the study bestowed upon it at present only suffices to permit the general relations of these regions being mentioned. A strong fusion of the acusticum systems occurs and since these are drawn cephalad under the cerebellum and the cerebellar crest is also somewhat concentrated, the appearance produced is that of two lobes of the cerebellum. The fasciculus communis is but weakly developed, especially the preauditory portion of it. The Xth arises by three large roots which penetrate the spinal fifth tract to reach their central connections, the two more cephalic also, passing through the acusticum which extends caudad to

this level. The lateral line nerve is small, but yet unexpectedly large when it is remembered that the lateral canal of the lateral line system is short; doubtless neuromasts in the epidermis occur. Cephalad of this root, one of medium size springs from the fasciculus communis system (IX?). VIIaa is very small; VIIb rather large.

*Eventognathi.* In the Cyprinidae we encounter forms already well known from the monograph of Mayser<sup>1</sup> and in them and the Catostomidae there exists so far as known to me, the greatest complexity of the oblongatal region among teleosts. The secondary fusion of the oblongata, involving in the two orders last mentioned the acusticum only, here includes also the preauditory portion of the fasciculus communis system and there is produced the *tuberculum impar* of earlier authors. For this fusion the great development of the fasciculus communis system and the nerves issuing from it, seems probably, in a degree, responsible; an increasing growth of this system under the limitations which the fusion of its cephalic portion imposes, produces apparently the monstrosity of the carp and sucker brain. A displacement of the acustic systems is also a necessary accompaniment of the growth and eversion of this inner region, and instead of being dorsal, it has been crowded cephalad, although when other things are considered, this may be shown to be more apparent than real. In the brains examined, however, a series of increasing complexity may be easily formed, which further studies will undoubtedly make more complete.

To Mayser's account of the cyprinoid brain little more can be added than to speak of the different modifications of the regions and their relations to the cranial nerves. No microscopical study of the carp brain has been made and Mayser's account has been taken as the source of information. *Notemigonus* is the simplest of the cyprinoid brains examined by the writer. The caudal beginning of the fasciculus communis systems is

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<sup>1</sup> Mayser examined many teleosts besides cyprinoids, and in the absence of any comparison or statement to the contrary, it has been assumed by some (and naturally) that the conditions described by him were typical of teleosts generally.



easily recognized and its development though great is not excessive (Fig. 14.). It soon assumes a dorsal position in the oblongata and the Xth nerve arises from it in two main divisions, both passing dorsad of the spinal Vth tract. Cephalad of the Xth the acusticum soon begins upon the side of the oblongata and at the caudal end of the fused preauditory portion of the fasciculus communis systems, the cerebellar crest appears. Two isolated fasciculus communis roots enter, one a short distance cephalad of the mass of the Xth nerve, the other (IX?) near the level of the entrance of the lateral line nerve (VIII post., Mayser). The *tuberculum impar* is a single mass, although a mesal groove on its dorsal side indicates its paired composition. From it fibers concentrate to form VIIaa which continues cephalad for a short distance as a round bundle after the tuberculum impar has been replaced by the fused acusticums. The roots in this region are much as in other forms and as described by Mayser, except that he recognized no root from the "tuberculum" acusticum except the VIIIth; VIIb and VIIaa as before, emerge together, VIIaa cephalad, VIIb caudad. The point of interest in *Notemigonus* is that the pre- and postauditory portions of the fasciculus communis system are directly continuous as in the teleosts before described and the postauditory or vagal portion does not overlap the tuberculum impar. The caudal limit of the communis fusion and the cerebellar crest upon the acusticum is nearly the same.

In *Notropis*, the common shiner, the vagal lobes are somewhat more developed and extend cephalad slightly around the tuberculum impar, so that in the same transection there is included the tuberculum impar, lobus vagi, and acusticum. In *Exoglossum* this is yet more marked and the structure is more carp-like (Fig. 26). The Xth as before, passes dorsad of the spinal Vth, occasionally breaking through it. An isolated cephalic fasciculus communis root (IX?) enters caudad of the entrance of the lateral line nerve.

In the carp the development and eversion of the vagal lobes (postauditory portion of the fasciculus communis) is much greater so that the spinal Vth is ventral rather than lateral and,

as Mayser shows, may be easily seen upon the ectal surface until the acusticum covers it up. A drawing of the dorsal aspect of the carp oblongata is shown in Fig. 2. (Comp. Fig. 4, of *Perca*.)

In *Catostomus* (Figs. 21, 22, 25) the development of the vagal lobes and tuberculum impar (fasciculus communis system) is carried a step farther. The vagal lobes are enormous and together with the cerebellum quite conceal the tuberculum impar and acusticums. The very large sensory portion of the Xth arises in two divisions and the motor farther ventrally but dorsad of, or breaking through the spinal Vth tract (Fig. 21). Farther cephalad another quite large root enters the lobus vagi after the acusticum has already appeared in transection (IX?). Figure 22 shows the overlapping of regions and Figure 25 may be compared with the similar section of *Perca* Fig. 19.

In none of the Eventognathi has a component of vagal fibers from the spinal Vth tract been certainly detected.

*In General.* The acusticum system in all these teleosts is not only dorsal but extends laterad over the side of the oblongata covering and submerging the spinal Vth tract which until its appearance is superficial. The general description of the structural appearance of the fasciculus communis in *Amia* applies also to teleosts.

In some forms the zone of small cells next the endyma is quite thick, six or seven cells deep. In *Amiurus* this zone is wanting and the cells are quite evenly dispersed through the region. When the system becomes greatly developed the dorsal and lateral growth involves structures covered primarily (typically) by endyma until they become ectal and pial. Closely associated with the communis system is the vagal motor nidus. In *Amia* (Fig. 16) and the simple teleosts (Figs. 10, 12, 13, 23, 24) this lies ventrad of the fasciculus communis and is easily recognized as forming no part with it, but in the cyprinoids (and suckers) the eversion of the fasciculus communis involves this region as well (Fig. 21.). Thus Mayser recognized in the lobus vagi of the carp 5 zones or layers,—(1) fibers of the va-

gus, (2) gelatinous substance, (3) secondary vagus tract, (4) motor nidus, (5) endyma. Between (1) and (2) might be interpolated the zone of small cells. Of these five layers only the first two would belong to the communis system; the others are involved because of the modification of this region. The tract recognized by Mayser and termed the "secondary vago-trigeminal tract" appears quite constantly in the teleosts (examined). It is a tract ventrad or ventro-mesad of the spinal Vth tract, formed by fibers coming from the fasciculus communis and going cephalad to a nidus at the base of the cerebellum (Rinden-knoten, Mayser) which communicates with its fellow by a dorsal commissure through the cerebellum.<sup>1</sup>

The relation the issuing vagal fibers bear to the spinal Vth is clearly due to mechanical advantage and the course they take is regulated by the position and development of their oblongatal center.

The communication of the two fasciculus communis systems caudad of the metatela, spoken of as the "*commissura infima Halleri*" appears constant. The caudal limit of the communis system was not always easy to determine. In most however (especially *Amiurus* and *Perca*), its limit was apparent, and Mayser's view that this as well as the spinal Vth was continuous with the gelatinosa of the myel, is questionable.

The distribution of the fibers of the root spoken of as the "lateral line nerve" has not been determined for any of the teleosts. It is, however, the undoubted homologue of the lateral line nerve in *Amia* and *Acipenser* in which its distribution has been shown. There is constantly found an isolated root from the fasciculus communis near or slightly caudad of the lateral line nerve, which I am inclined to think represents the sensory portion of the IXth. The relation in *Amiurus* resem-

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<sup>1</sup> Mayser believed the secondary vago-trigeminal tracts decussated through the cerebellum. From the conditions in *Amiurus*, which has been more especially studied, this does not seem to be the case; the two tracts terminate and the nidi in which they terminate are connected by a dorsal commissure through the cerebellum.



bles that in *Amia* and the correctness of the homology seems probable.

An estimate of the absolute amount of development these systems have undergone in the Eventognathi and the extent to which it alone has influenced the morphology of the oblongata appears as yet impossible, because all the necessary data are not known. A simple concentration of structure whether due to intrinsic or extrinsic causes, might in some cases appear as a greater development. The fusions, also, are unexplainable until a study of the development of the oblongata has been made in which are carefully considered the conditions of growth and the relation of the oblongata to the cranial wall and ear.

#### CONCLUSION.

To sum up, then, the result of the foregoing observations, the morphologically dorsal region of the oblongata is composed of three systems, the spinal Vth tract, the fasciculus communis system and the acusticum. The first is the direct representative in the oblongata of the dorsal horn and associated columns of alba of the myel; the other two regions appear peculiar to the oblongata, the first typically more mesal, the second dorsal and capped by a caudal extension of the molecular layer of the cerebellum. The spinal V furnishes all (?) the sensory fibers of the trigeminal nerve and, in *Amia*, *Perca*, *Amiurus*, *Roccus* and *Lepomis*, at least, a small contingent of fibers to the Xth (possibly in Ganoids (*Amia*), to the seventh also). From the *fasciculus communis* spring the larger part of the ganglionated IX and X and VII; while from the tuberculum acusticum, the nerves supplying the ear and the organs of the lateral line system. In *Amia*, and it is probably so for other Ganoids, the spinal V is superficial, in other words the acusticum is wholly dorsal. In Teleosts the acusticum also extends laterad covering and submerging to a greater or less extent the spinal fifth tract. The first condition, that in *Amia*, is evidently the simpler. In Urodeles and *Petromyzon* (Ahlborn) the spinal (ascending) V occupies a superficial position. The results of His and Minot on

the development of the oblongata of the human brain show a similar submergence of the fasc. solitarius, at first a superficial tract, by the ventral growth of dorsal regions (Rautenlippe),<sup>1</sup> and I have no doubt that when the development of the oblongata in Teleosts is studied with this point in view, a similar change will be found to take place here and at some stage the spinal V tract to be superficial as in Urodeles and Ganoids.

Among Teleosts there exist wonderful modifications in the development of these systems. The simplest condition is found in the two representatives of the order Haplomi which were examined, *Esox* and *Fundulus*, where the regions have as great a cephalo-caudal extension as in Ganoids and no fusions occur. In the Acanthopteri there is a fusion of the tubercula acustica across the meson, constant in the representatives of the four of its families that were examined. In *Clupea* the acusticums are fused and more concentrated, so that the appearance is that of a lobe of the cerebellum. In the representatives of the other two orders, there is a more or less marked development of the *communis* system, especially of the preauditory portion of it, together with a more or less evident concentration of oblongatal structures (cephalization) which has not yet been properly estimated. *Amiurus* is simplest, with no secondary fusion of any portion of the oblongata, although the preauditory portion of the fasciculus communis tract is greatly developed. In the Eventognathi there exists an increasing complexity in the structure of the fasciculus communis, and fusion of the cephalic end (preauditory), of the two tracts as well as of the acusticums occurs. In *Notemigonus* the relation is simplest since here the lobi vagi do not overlap the fused lobi trigemini as occurs in other cyprinoids, notably *Cyprinus*. In the Catostomidae, the development is more marked. Here (*Catostomus*) the enormous lobi vagi extend cephalad over the lobi trigemini so as to nearly or quite conceal it and the fused acusticums, and there is a

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<sup>1</sup> "Within a few days the Rautenlippe unites with the main fold of the zone and continues to grow toward the median ventral line passing outside of the tractus solitarius, which thus becomes buried, and, instead of lying superficially, is thereafter deep below the outer surface." Minot, p. 666.

third though small fusion of the lobi vagi. It is a difficult matter to represent by diagram the successive degrees of complexity in the teleosts which lead up to the sucker (*Catostomus*) as their climax. It has however been attempted in Figs. 30-33. When other orders and families of teleosts are examined other modifications and degrees of development will doubtless be found to exist, and in other families of the orders represented here; while in other genera of the families, conditions may be found which will bridge over the differences between the families or orders, so that any generalization from the relations so far found constant, is unsafe.<sup>1</sup> The various developments of the nerve centers are too clearly dependent on the extent and functional activity of the regions or organs innervated to have much morphological value attached to them. The cause of the fusions that occur seems a difficult matter and no attempt has been made to determine in how far the interference of the cranium or ear during development may be responsible. Surely however from such a form as *Amiurus* with widely separated acusticums, it would be hard to derive a cyprinoid with fused acusticums and lobi trigemini.

Strong's work on the cranial nerves of Amphibia has been previously mentioned as the direct inspirer of these observations and it seems to the writer a most helpful step toward the comprehension of the cranial nerves of vertebrates in offering grounds for the homologization of the nerve roots throughout the vertebrate series, and thereby the regions of the oblongata with which they are associated; and in the determination of the components of the nerves, their origin and peripheral distribution, to assist the facts of development in the solution of the problems of the morphology of the vertebrate head and

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<sup>1</sup> A careful study of the brain of the different orders and families of the teleostei has never been made and seems to be a piece of work much needed. Mayer undertook such a study of the teleost brain to make it the base of classification. His work was evidently superficial and his figures indefinite or incorrect. The Herricks in this country have done much in the study of the teleost brain. The bony fishes would certainly offers a good field for testing the value of the brain in taxonomic work. The results so far gained suggest that some interesting results may be gained.



the comparison of spinal and cranial nerves. Strong's conclusions as to the components of the cranial nerves of Ichthyopsida may perhaps be best given in his own words: "We have seen that in the cranial nerves of the higher fishes there are three kinds of cutaneous nerves distinguishable by peculiarities of their fibers, of their distribution, and of their internal origin, *i. e.*, (1) mixed fibers of a general cutaneous character continuous with the posterior columns of the cord, (2) coarse fibers innervating the lateral line organs and terminating centrally in the differentiated tuberculum acusticum, and (3) fine fibers innervating the terminal buds (coarse in Selachians and innervating the ampullae?) and terminating centrally (principally) in the lobus trigemini. The latter, *i. e.*, (3), is possibly not completely differentiated. Among the Cyclostomes, it seems probable that this specialization has not been carried so far, but this is not yet sufficiently known." In addition and disregarding here the motor (non-ganglionated) components was recognized the *fasciculus communis* component, composed of fine myelinic or amyelinic fibers which constitute the (visceral) nerves of the alimentary tract. Speaking of its great development in fishes, he says: "Its great development in fishes is correlated with the development of the gills, and where these are in process of reduction or lost it is correspondingly reduced" (p. 190). Thus then in addition to the motor nerves, there exist in the cranial nerves, components as follows:—(a) general cutaneous, (b) lateral line, (c) end-bud, and (d) splanchnic; and these having their central connections in or through (a) the ascending V (spinal V tract), (b) tuberculum acusticum, (c) lobus trigemini and (d) lobus vagi—*fasciculus communis*.

In regard to the relation of the last two regions, the accounts of different writers introduced difficulties that prevented conclusions at all definite being reached. The difficulty, upon a study of the oblongata, shows itself to be due largely to the careless application of the same term in teleosts and elasmobranchs to structures which are not homologous, and for this obscurity both Goronowitsch and Mayser appear in a degree

responsible. Goronowitsch, in the readiness with which he recognized the fibers arising from the so-called lobus trigemini in *Acipenser* as fine as compared with the fibers from the dorsal tracts, favored by his determination to find in the cranial nerves the dorsal and ventral roots of the spinal nerves; and Mayser, in applying (first) the name lobus trigemini previously used in the elasmobranch brain to a structure in the cyprinoid brain without determining their complete homology.

Under such circumstances attempts to completely homologize the nerves in Ichthyopsida must fail without a recognition of this trouble, and as soon as it is recognized many points before inexplicable are cleared up.

In Elasmobranchs there exists upon the dorsal side of the oblongata an elevated region which is simply a continuation caudad of the *corpus restiforme*, and to this the name of lobus trigemini was quite generally applied (by Miklucho-Maclay; Viault, Rohon, Gegenbaur). Since it is a direct continuation of the corpus restiforme, that name, as used by some (Stannius) also includes it. It is partially covered by a caudal extension of the molecular layer of the cerebellum which also covers the dorsal tracts laterad of it. Beneath it a large nerve root arises, the most dorsal of the nerves of the V-VII complex. This is undoubtedly the nerve from the corpus restiforme of Stannius innervating the 'mucous' canals. Ewart describes the most dorsal of the nerves distributed to the lateral line system in *Lae-margus* as the *ophthalmicus superficialis*. "This nerve arises by a large root from the so-called trigeminal nucleus which occupies the most dorsal portion of the medulla." It communicates freely with the buccal. VIIc of Strong '94 in *Galeocerdo* seems to be the same root.

It seems probable that the "lobus trigemini" of *Acipenser* (and other sturgeons, probably) is the same structure found in sharks and the nerves are homologous. In examining transections through this region of the *Acipenser* brain, the impression was strong that there had been a partial folding in of the cerebellar crest and fusion of the two surfaces. The occurrence of large (Purkinje) cells on both sides of the cerebellar crest

strengthens the belief. The comparison of sections of *Acipenser* with the figures of Rohon and Sanders of the corresponding region of the shark brain indicates that the structure is the same in both. The homology entertained, but rejected, by Strong of *Trig. II dors.* with VIIu of Osborn in *Cryptobranchius* (my VIIb' in *Necturus*) springing from an island of ground substance upon the dorsal side of the oblongata, is perhaps worthy of being further considered. It was rejected by Strong mainly (apparently) because the conflicting use of "lobus trigemini" necessitated other homologies. Were it correct there would persist in reduced state in shark-like ganoids and the larger urodeles the remnant of an elasmobranchian structure (*corpus restiforme?*). Therefore, not to devote more space to it here, it would seem to me that a consideration of the relations of the "lobe" and its nerve root and comparison with ganoids leaves it highly probable that the root from the lobus trigemini in sharks is the homologue (in part) of VIIb Strong, the lateral line component, and the "lobus trigemini" will prove on investigation to be a modified portion of the acusticum system.

In teleosts the lobus trigemini is but the enlarged cephalic portion of the fasciculus communis system; fused in the Elenotognathi, unfused in *Aminurus* (Nematognathi?), while in other teleosts examined no lobus trigemini as a special hypertrophy exists. The root from this lobe, the "dorsal geniculate root of the Vth" is the homologue of VIIaa in Amphibia and is present whether a lobus trigemini as such exists or not. This is not saying, however, that they are in each case exactly equivalent.

In view of the foregoing statements the following may give help on some of the points and problems raised by Strong. In the first place, the nerve of Goronowitsch from the "lobus trigemini" of *Acipenser* is not the homologue of the geniculate V of teleosts which is the representative of his dorsal root of the seventh (I'rd.) from the fasciculus communis (lobus vagi). The recognition of TIIId. as a lateral line root clears up the difficulties occasioned by its distribution to the ophthalmicus su-



perforialis VII, buccal and otic and hyomandibular. We should expect the root from the "lobus trigemini" of sharks to be coarse fibered if it innervates the lateral line organs. If Ewart is correct, the Ampullae of Lorenzini would be more closely related to the lateral line organs and not representatives in Elasmobranchs of end-buds of higher forms.<sup>1</sup> In Amphibia, though no differentiated lobus trigemini exists, it is represented morphologically by the cephalic portion of the fasciculus communis in connection with the preauditory root from this tract, VIIaa Strong. Of the three alternatives offered in the interpretation of the lobus trigemini and the innervation of the end-buds, when it is recognized that the lobus trigemini and lobus vagi are but differentiated parts of the fasciculus communis tract, the first two lose their point and the third, which Strong regarded as most probable, stands, with this modification, that the lobus vagi and lobus trigemini, of teleosts, instead of being distinct structures partially equivalent, are but the differentiated pre- and postauditory parts of the same system. The question of the innervation of the end-buds remains as difficult and as far from a satisfactory solution as before. It is quite possible that, as Strong suggests, two kinds of fibers from different portions of the fasciculus communis tract may have distinct distributions—one end-bud and the other splanchnic.

The view apparently entertained by Allis ('95) that the fasciculus communis gives rise to fibers distributed exclusively to end-buds is certainly not correct, since very much the larger part of the sensory (ganglionated) fibers of the vago-glossopharyngeal spring in *Amia* (and in other Teleostomes) from that tract.

That the end-buds on the head of teleosts receive their innervation from both pre- and post-auditory portions of the tract is undoubtedly true from the investigations of Wright, Allis and Strong. In *Amiurus* (Wright) and the carp barbel end-buds in the skin of the head are plentiful, and doubtless when other cyprinoids and suckers are examined the end-buds

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<sup>1</sup>Since they are innervated by the same nerves as are the lateral line organs. See also Cole, '96.

will be found equally or more abundant, and in forms with a weak development of the fasciculus communis system, they will be few or wanting in the skin. In *Amia* the preauditory communis component forms the palatine nerve and contributes fibers to the *rami maxillares inferior* and *superior* which go to regions where end-buds occur (Allis '95).

In *Amiurus* (Wright '84) from the fasciculus communis (Lob. trig.) component are derived the most of the fibers of the (1) *ramus lateralis trigemini*, (2) the *ramus ophthalmicus profundus*, from which the nasal barblets receive their innervation, (3) the *ramus maxillaris*, which innervates the large maxillary barblet and (4) the *ramus mandibularis*, innervating the mental barblets, and (5) the palatine and cutaneous palatine nerves. These facts, while they indicate the innervation of end-buds from the fasciculus communis component, raise many difficult questions bearing on the basis of homology of cranial nerves in higher and lower forms. While the lobus trigemini root was considered as part of the Vth, the distribution of its fibers to form such recognized trigeminal nerves as the *ophthalmicus profundus* and *mandibularis* and *maxillaris* would present no great difficulties; but they do appear as soon as it is recognized that the so-called geniculate root of the Vth of teleosts is the homologue of VIIaa (Strong) of Amphibia. In *Amia* the difficulty is as great as in *Amiurus*.

It is however only when the nerve is regarded as a unit with constant central connections (roots) and constant branches (rami) that the difficulty has full force. Certainly suggestive in this connection is Miss Platt's work on the development of the peripheral nervous system in *Necturus*. The idea that may be gained there,<sup>1</sup> broadly stated, is that the central and peripheral

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<sup>1</sup> "I will go no further than to add that, as far as the lateral line organs are concerned, their fibers choose the nearest and most direct path to the auditory centers in the brain, which seem to be also the centers of the entire lateral line system, yet both development and comparative anatomy tend to show that it is a matter of little moment whether these fibers enter the brain by one nerve root or another" Platt, p. 505.

"This study, therefore, leads to the conclusion that it is of little moment whether the motor and sensory fibers belonging to the primitive nerves of any

terminations of a nerve fiber are important and constant, while the intermediate course is due more to advantage and may vary. Viewing this from the standpoint of two opposed theories of nerve development and the relation of nerve fiber and ganglion cell, it would be in one case the central and in the other the peripheral region that is the center of growth and constant; that is, in the first case the ganglion would be fixed and the course the outgrowing neurites took to reach their destination would be the easiest or shortest path; in the second case, the nerve fiber, developing as a chain of cells from the ectoderm would take the easiest or shortest course to the appropriate brain-center. It is the latter view of nerve development that Miss Platt's researches support. Discussion of this point will be avoided here; however, it seems that in certain fishes end-buds occur in the skin of the head and in the mouth, and the nerve-fibers entering the brain through a root near the VIIIth nerve, reach their peripheral destination (the end-buds) through numerous nerves. In Amphibia (and higher forms) the end-buds are confined to the mouth and the fibers of this root are distributed only to pharyngeal nerves.

Turning to the brain of Urodeles (*Necturus* etc.) in view of the conditions in fishes (especially *Amia*), it is comparatively safe to homologize the whole region dorsad of the spinal Vth tract with the *acusticum*; this is sustained by the ental origin of the VIIIth nerve and the nerves of the lateral line system. The tailless Amphibia cannot be included yet. Very interesting would be a study of the development and structure of the oblongata of the Anura to determine the regions and their homology. It might facilitate comparison between higher and lower forms which seems unsatisfactory. The entire homology of the fasciculus communis system with the *tractus solitarius* still

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segment enter the brain by one root, by two roots, or by several, the position of the nerve-root being in great measure an expression of the co-ordinate relations which the central nervous system subserves. The morphological value of the nerve comes from without and 'the metameric arrangement of the peripheral nerves is probably not primary, but occurs in adaptation to the segmentation of the structures they supply' (Froriep, 14, p. 590)." Platt, p. 540.



appeals to the writer as unsafe, and the opinion expressed before ('95) is adhered to,—that the data for a full comparison of higher and lower forms are insufficient.

#### SUMMARY.

The annexed table may summarize the nerve components of the typical forms examined, and the following points recapitulate the general results of the study of the oblongata, illustrated by diagrams of figures 27-36.

1. Three systems constitute the centers for the ganglionated (sensory) nerves of Teleostomes and form the dorsal portion of the oblongata: they are, (1) the spinal Vth tract (system), (2) the fasciculus communis system and (3) the acusticum system.

2. The first gives fibers to the Vth nerve and in *Amia*, *Amiurus*, *Perca*, *Roccus* and *Lepomis* at least, a small contingent to the Xth.

3. The second furnishes fibers to the VII, and IX and X (visceral and end-bud).

4. The third furnishes fibers to the VII and IX and X (lateral line system), and gives rise to the VIIIth.

5. The lobus trigemini and lobus vagi of some Teleosts are but the differentiated pre- and post-auditory portions of the fasciculus communis system.

6. The "dorsal geniculate root of the Vth" of teleosts is the homologue of VIIaa (Strong) of Amphibia.

7. The lobus trigemini of Elasmobranchs it is believed will prove more closely related to the acusticum of ganoids and teleosts; it is clearly the caudal continuation of the *restis* of the elasmobranch brain.

8. No secondary fusions of regions were found in *Amiurus* (Nematognathi) and *Esox* and *Fundulus* (Haplomi).

9. Fusion of the acusticums occurred in the Acanthopteri (4 families) and in the Isospondyli (*Clupea*).

10. Fusion of the acusticums and lobi trigemini is found in the Cyprinidae.

11. *Catostomus* (Catostomidae?) showed in addition to the fusions in the cyprinidae, a fusion of the lobi vagi.

12. The acusticum was in every case covered by a caudal extension of the molecular layer of the cerebellum.

NERVE	COMPONENT	DISTRIBUTION	CENTER	AMPHIBIA	GANOIDS	TELEOSTS		
				NECTURUS	AMIA	PERCA	AMIURUS	CATOSTOMUS
V.	1.	general cutaneous (?)	Sp. Vth. tr.	present	present	present, well defined	present	present
	2.	motor (?)	mesen.	strong				
	3.	motor	motor nidus*	*				
VI.	1.	motor	motor nidus					
VII.	VIIab	motor	motor nidus					
	VIIb.	lateral line system	acusticum	present, 2 roots	present, 1 root	present	present	present
	VIIaa	end-bud and visceral (?)	fasciculus communis	"	"	" medi-uni	" very large	" large
VIII.	1 (2)	ear	acusticum	present	present	present	present	present
IX.	1.	lateral line system	acusticum	present	1 root	present	present	present
	2.	end-bud and visceral (?)	fasciculus communis	"	present	" (?)	" small	" (?)
	3.	motor	motor nidus					
X.	1.	motor	motor nidus	present	present	present	present, quite large	present, large
	2.	end-bud (?) and visceral	fasciculus communis					
	3.	general cutaneous (?)	sp. Vth. tr.	"	present small	" medi-uni	present, small	(?)

\*The motor nerves are not discussed in this paper, and so are not regarded in the table. The nerve components are given as they were found in the study of the brain in these forms.

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## EXPLANATION OF FIGURES.

It is impossible to illustrate this paper adequately since of each form several figures at different levels would be desirable in order to show the gradual changes undergone in passing from the myel into the oblongata and the appearance of the structures discussed in the foregoing. Dorsal views of the oblongata of *Amia*, *Amiurus*, *Perca* and *Cyprinus* are given. Series of 6 figures of transections of the oblongata in *Amia*, 5 in *Amiurus* and two *Perca* are given to illustrate the modifications, to which are added 8 diagrammatic figures of other forms for comparison. All figures are drawn by the aid of the microscope and camera lucida except figures 2 and 5 and the diagrams of plate V. Figure 2 is based upon a photograph.

## ABBREVIATIONS.

- |   |   |
|---|---|
| <i>ac.</i> —acusticum (system).   | <i>ni.</i> —motor nidus of the Xth nerve.   |
| <i>cbl.</i> —cerebellum.  | <i>p. l. f.</i> —posterior longitudinal fasciculus.                                     |
| <i>cbl. cr.</i> —cerebellar crest.  | <i>sp. V.</i> —spinal (ascending) Vth tract.  |
| <i>c. d.</i> —dorsal cornu.   | <i>s. t. tr.</i> —secondary vago-trigeminal tract.                                      |
| <i>cm. i.</i> —commissura infima Halleri.                                       | <i>t. i.</i> —tuberculum impar (fused preauditory part of fasciculus communis systems). |
| <i>f. c.</i> —fasciculus communis (system).                                     | <i>VIIaa.</i> —preauditory fasciculus communis root.                                    |
| <i>l. l.</i> —lateral line nerve.   | <i>VIIab.</i> —facial proper.   |
| <i>l. t.</i> —lobus trigemini (preauditory portion of the fasciculus communis). | <i>VIIb.</i> —acusticum root.   |
| <i>l. v.</i> —lobus vagi (postauditory portion of the fasciculus communis).     | <i>Xm.</i> —motor root of the Xth nerve.  |
| <i>M. c.</i> —Mauthner cell.  | <i>Xs.</i> —sensory root of the Xth nerve.  |
| <i>Mesen.</i> —Mesencephal.   |   |
| <i>myc.</i> —myelocœle.   |   |

## PLATE I.

*Fig. 1.* Dorsal view of the oblongata of *Amia*. The metatela is removed in this and the following aspects since it would interfere with the regions desired to be shown.

*Fig. 2.* Dorsal aspect of the oblongata of *Cyprinus*. Metatela removed. The brain cavities were injected with alcohol and the vagal lobes (*l. v.*) were apparently somewhat spread apart thereby. The cerebellum has been removed and the cut surface only is seen.

*Fig. 3.* Lateral aspect of the oblongata of *Amia* to illustrate the superficiality and course of the spinal V tract to the Vth nerve.

*Fig. 4.* Dorsal aspect of the oblongata of *Perca*. The cerebellum has been removed and the cut surface alone is seen.

*Fig. 5.* Dorsal view of the oblongata of *Amiurus*.

*Fig. 6.* A transection through the myel of *Amia* near the brain. The dorsal cornua of the cinerea at this level are considerably larger than in a section of typical myel.

*Fig. 7.* Transection of the myel of *Amiurus*.

## PLATE II.

*Fig. 8.* *Amiurus*. Transection of the myel (oblongata?) near the metatela showing the enormously enlarged dorsal cornua.

*Fig. 9.* *Amiurus*. Transection immediately caudad of the metatela through the beginning of the fasciculus communis system (*cm. i.*). The dorsal cornua have diminished slightly in size and the spinal Vth tract has appeared.

*Fig. 10. Amiurus.* Transection farther cephalad, the fasciculus communis is dorsal (*l. v.*), the spinal Vth and the almost entirely reduced dorsal cornua are displaced.

*Fig. 11. Amiurus.* Transection at the level of the exit of the VIIth roots. Intermediate between this and figure 10 is figure 24 at the entrance of the IX?, showing the developing acusticums.

*Fig. 12. Perca.* Transection of the oblongata at the exit of the Xth nerve. A component from the spinal Vth tract is shown.

*Fig. 13. Amia.* Transection through the myel showing the enlarged dorsal cornua. (Comp. fig. 6 and figs. 15-18.)

*Fig. 14. Notemigonus.* Transection through the oblongata at the exit of the Xth nerve.

### PLATE III.

*Fig. 15. Amia.* Transection of the oblongata at the first (recognizable) appearance of the fasciculus communis system.

*Fig. 16. Amia.* Transection farther cephalad near the caudal appearance of the acusticum and the cerebellar crest.

*Fig. 17. Amia.* Transection at the level of the IXth.

*Fig. 18. Amia.* Transection of the oblongata at the exit of the VII-VIIIth nerves.

*Fig. 19. Perca.* Transection of the oblongata caudad of the VIIIth showing the fusion of the acusticums.

*Fig. 20. Esox.* Transection of the oblongata at the exit of the VIIIth.

### PLATE IV.

*Fig. 21. Catostomus.* Transection of the brain at the exit of the Xth. A fusion of the vagal lobes is shown. (Comp. figure 14 of the corresponding level in Notemigonus.)

*Fig. 22. Catostomus.* Transection farther cephalad including the tuberculum impar, the acusticums and the cephalic projection of the lobus vagi.

*Fig. 23. Roccus.* Transection of the oblongata at the exit of the Xth nerve.

*Fig. 24. Amiurus.* Transection of the oblongata at the level of the entrance of IX?

*Fig. 25. Catostomus.* Transection of the oblongata farther cephalad than figure 22 where the tuberculum impar has been replaced by the fused acusticums.

*Fig. 26. Exoglossum.* Transection through the oblongata showing slight overlapping of the tuberculum impar by the lobus vagi and the first appearance of the acusticum.

### PLATE V.

Ten diagrams to illustrate the regions and nerves discussed which are demarcated in different colors.

*Figs. 27-29.* Diagrams of the sensory (ganglionated) oblongatal nerve roots in *Necturus* (Amphibia) *Amia* and *Amiurus*.

*Figs. 31, 30, 32, 33.* Diagrams of the oblongatas of *Amia*, *Perca*, *Notemigonus* and *Cyprinus* to illustrate the increasing complexity and associated fusions. The left side in *Perca* and *Amia* are shown as though the fasciculus communis system were exposed,—as if the covering part of the acusticum had been dissected away. (Comp. figs. 1 and 4.)

*Figs. 34-36.* Transections through the oblongata of *Amiurus*, *Amia*, and *Perca* respectively. Fig. 34 caudad of VIIIth; fig. 35 near the IXth and fig. 36 cephalad of the Xth.

## THE ENCEPHALIC EVAGINATIONS IN GANOIDS.

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(*With Plate VI.*)

The great interest attaching to the extent and interpretation of the membranous roof of the vertebrate brain cephalad of the postcommissure, and the number and significance of the outgrowths occurring in this region may serve as an excuse for the isolated publication of a few facts upon the latter in Ganoids, especially since the presentation of the results of a more general study of the ganoid brain seems somewhat remote.

The new and important points are two: (1) the presence in the adult *Amia* of the first epiphysial vesicle of Hill and its innervation from the left habena; and (2) the existence in *Amia* and *Lepidosteus* of lateral cephalic and caudal extensions of the cavity caudad of the *velum transversum* of Kupffer, constituting considerable diverticula. More emphasis it is felt should be laid on the existence of the "dorsal sack" and the presence of the paraphysis as distinct structures. A word may be added upon the metaplexus in *Lepidosteus* which presents some interesting features in connection with the diverticula from the diatela.

*Epiphysis.* Great interest has always attached to this structure, so constant in the vertebrate series, as the remnant in a greater or less degree of preservation, of a sense-organ once of importance in vertebrate ancestors. Recently fresh interest has been added by the studies of numerous observers which go strongly to show (though not conclusively as yet, it is felt) the presence of two, or possibly more, evaginations from this region of the brain roof. By Hill, Studnicka, and Locy is entertained the view that it is the more caudal of these, the epiphysis proper, which is most developed in the lamprey and persists



in all craniota in a more reduced state; the cephalic is the "second epiphysial vesicle" in *Petromyzon*, the parapineal organ of Studnicka ('95). It occurs in embryo teleosts and *Amia* (Hill), and in reptiles becomes separated from the brain as the well known parietal eye of lizards. There is, however, no case so far as known to me where they might not be interpreted as but modified parts of the same primary evagination,<sup>1</sup> were it not for the observation of Locy of three pairs of depressions upon the medullary plate of the shark embryo; the first enter the optic evaginations; the second he traced to the epiphysis; while the third pair was lost.

As has been said by others, the need now is the accumulation of facts showing the relations in this region of the brain in a wide range of forms, especially embryologic data which will throw light on the first appearance of these (or this) evaginations in the various forms. It is as contributing a little to the interpretation of these structures that the following is offered. It has just been stated that Hill has already described the existence of two epiphysial structures in the embryo *Amia*. The cephalic evagination (epiphysis I) in embryos of 10 mm. length is an ellipsoid sack lying upon the left side of the epiphysial stalk (epiphysis II); its cavity is connected with the cavity of the brain. Likewise in 13 mm. *Amia* the cavity is in communication with the brain, but in embryos 15 mm. long the connection is severed and epiphysis I lies upon the left side of epiphysis II. It appears that the adult or later embryos were not examined. In *Salmo* (the teleost more especially studied; others were *Catostomus*, *Stizostedion* and *Lepomis*) the connection is severed in 13 mm. embryos; in 25 mm. *Salmo* (160 days old) the cavity is obliterated and in 2 year fish it is recognizable only in

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<sup>1</sup> Leydig, Beraneck and Francotte state that two distinct outgrowths from the roof of the diencephal in reptiles occur. Klinckschröm, Selenka and Sorensen however think there is but one evagination. Accessory parietal eyes which have been observed in certain lizards appear variable in number and cannot yet be interpreted. Likewise in *Petromyzon*, earlier stages of the development of these structures are wanting and the cephalic vesicle may prove, as believed by some, to be derived from the caudal.

one fish as a small mass of cells lying to the left of the epiphysis (epiphysis II). In adult *Amia*, however, this structure persists as a hollow vesicle closely applied to the left of the epiphysis (Epiph. II) and with it enveloped by the dorsal sack in which they are suspended as by a fold. Epiphysis I lies almost directly dorsad of the supracommissure and receives a strong fasciculus of non-medullated fibers from the left habena (Fig. 1). This point is important since it strengthens the homology of this with the parapineal organ (Studnicka) of *Petromyzon* which has been found to have fiber connection with the left habena.<sup>1</sup>

*Lepidosteus* (adult) was examined and no trace of the epiphysis I was found although a small cluster of cells in the proper location possibly represented it in much reduced state (as in 2 year *Salmo*, Hill). No trace of it has been found in adult *Polyodon* or *Acipenser*, in which this region was subjected to examination by Studnicka '96 and Goronowitsch. Kupffer does not show it in embryo *Acipenser*.

*Dorsal Sack.* Goronowitsch, I believe, was the first to employ this term. It has since been employed by Mrs. Gage, Herrick, Humphrey and Wilder, and seems preferable to the other terms applied to this region of the brain, which seems worthy of a distinct name, whatever its morphologic value.<sup>2</sup> It is the cavity included beneath the diatela caudad of the velum transversum, Kupffer. In Ganoids, especially the sturgeons, it is voluminous, and as described above, in *Amia* it envelops the epiphysis which thus appears suspended in it by a mesal fold. It does not seem to be a true evagination, such as the epiphysis and paraphysis, but a dorsal extension of the dia-coele, due perhaps entirely to mechanical causes and given the

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<sup>1</sup> The suggestion of Locy that the difference in size between the left and right habenas was due to this innervation, fails, since it is the right and not the left which is the larger, and whatever the cause of this, it is associated with a similar difference in the Meynert's bundles springing from them. This peculiar asymmetry in *Petromyzon* also exists in *Amia*.

<sup>2</sup> Synonymy; Zirbelpolster, Burckhardt; Parencephalon, Kupffer; Postparaphysis, Sorensen; Vesicle of the Thalamencephalon, Parker and Balfour; Recessus praepinealis, Leydig (?).

appearance of an evagination by the velum. The last structure has been recognized in Amphibia and Reptilia and appears of morphologic value. By some it has been assumed as the boundary between the prosencephal and diencephal. In *Amia* it passes ventrally immediately caudad of the cerebral lobes, which slope at their caudal end and hence give the dorsal sack more volume. The velum is attached to the recurved edge of of the cerebral lobes and therefore the same condition of the latter would render greater the extent of the velum. The prominence of the velum in Ganoids may be in part due to the recurved condition of the cerebral lobe at its caudal end.

The membranous roof caudad of this fold has a modification which when first observed was rather startling. There occurs on each side a lateral extension of the cavity just caudad of the velum, forming diverticula which divide into two limbs, caudal and cephalic. The latter extends cephalad just ventrad of the recurved edge of the cerebrum as far as the olfactory lobes (Figs. 3, 4). The caudal limb is even more extensive: closely applied to the side of the mesencephal, it reaches the cerebellum and the ventral portion passes farther caudad encountering the fifth nerve which divides it into a short dorsal portion and a longer ventral one, which in some brains at least attains the level of the ninth nerve, closely applied to the ventral aspect of the oblongata.

*Lepidosteus* resembles *Amia* closely. The relations are somewhat modified however by the different shape of the cerebral lobes. These do not slope away at their caudal ends which are more closely applied to the geminums and more nearly perpendicular to the dorsal surface. The recurvature of the dorsal edge is not so great (fig. 2). All this limits the capacity and extent of the dorsal sack and the size of the velum. The caudal extension of the dorsal sack upon the mesencephal is somewhat greater than in *Amia*. The epiphysis in *Lepidosteus* is in its proximal part enveloped in the dorsal sack and extends caudad to bend cephalad forming a V. In *Amia* the epiphysis first passes cephalad then caudad and again cephalad, performing thus a sigmoid curve. The lateral diverticu-



lum caudad of the velum exists, but the closer approximation of cerebrum and geminum renders it far less conspicuous. The slightly recurved lobes also do not form the interval occupied in *Amia* by the cephalic portion of the diverticulum, and this in *Lepidosteus* is flatter. The caudal portion is also extensive and reaches at least to the cerebellum, but here a complication existed which prevented the caudal limit being ascertained; namely, the presence of similar lateral extensions of the membranous roof of the metencephal. Some distance caudad of the metatela lateral pockets appear upon the sides of the oblongata (or myel) which farther cephalad are seen to be from the metaplexus. From the point where they join the metaplexus cephalad there is a lateral extension of the cavity, or rather more correctly, a series of lateral extensions which in some regions reach to the ventral surface of the brain and almost meet each other at the ventrimeson (Fig. 5). There is also a projection of the metatela over the surface of the cerebellum.

The membranous roof of the prosencephal, the mesal fold from it, the dorsal sack and velum and the metaplexus in *Amia* and *Lepidosteus* are lined with an endymal epithelium of large columnar cells which are of the appearance characteristic of secreting cells; the nucleus is situated in the base and the cell body stains but lightly, resembling some mucous cells. The lateral diverticula are also lined by such cells, but only on their ectal side; the ental side toward the brain, being very delicate and lined with flattened cells. The membranous roof of the fore-brain, the velum and mesal fold are all richly supplied with blood vessels, or blood spaces, and the ectal surface of the diverticula is also similarly supplied. We cannot doubt that the columnar cells of the membranous portions of the brain roof are of use in the elaboration of the coeliolymph. Vascular portions of the telas of the brain, generally appearing as plexuses, are of quite usual occurrence, and must have an important function in the nourishment of the organ. The only explanation of these diverticula that appeals to me is that they are for the increase of secreting surface. This may be accomplished in either of two ways, by reduplication, as in the forma-

tion of folds and villi in the alimentary tract and plexuses in the brain; or by expansion, and it seems to be the latter method adopted in the brain of *Amia*. In the formation of folds or plexuses it is necessary for the blood vessels to intrude into the brain cavity; here the cavity has, as it were, come out to the blood vessels. The same seems to be true of the metaplexus, of *Lepidosteus*, and it is interesting to note that, whereas in *Amia* the metaplexus is richly folded, in *Lepidosteus* it is entirely smooth save for small folds at the sides.

Careful examination of other Ganoids may reveal conditions much like those existing in these two. Both *Polyodon* and *Acipenser* brains are covered with a dense layer of connective tissue which may involve such outgrowths of the diatela as here described. Studnicka has recently reported that in *Polypterus* the dorsal sack extends caudad as far as the cerebellum and the description and figures of Waldschmidt suggest strongly even an exaggeration of the conditions in *Amia*.

*Paraphysis*.—The presence of the paraphysis in *Amia* has already been noted by Hill. In the adult it opens into the cavity just cephalad of the velum (Fig. 4) and possesses many tubular diverticula which occupy space in the velum (Fig. 3), in the membranous roof of the prosencephal and in the caudal part of the mesal fold. These are lined with a cubical or columnar epithelium which, it is important to note, is of a different appearance and easily distinguishable from the cells of the dorsal sack and membranous roof. The paraphysis does not seem to be a sack caused by or of the same nature as a plexus; on the other hand, neither is it an evagination of the same appearance and significance as the epiphysis and the view of His, Kupffer, and Leydig ('96), that it really is an epiphysis, does not seem correct; the terms employed by them, vordere Epiphysis and Epiphysis I, should not be confused with the anterior epiphysis or epiphysis I used by others and in this article. The paraphysis seems a structure in itself. The cells have indeed the appearance of secreting cells, but of a nature different from those of the surrounding epithelium.

The paraphysis also exists in *Lepidosteus*, appearing much

as in *Amia*. *Acipenser* (Kupffer, Epiphysis I) and *Polyodon* (Studnicka, '96) both possess it as doubtless do other Ganoids.

In cephalo-caudal succession we find then, on the mesal section of this region of the brain of *Amia*, the mesal fold of the prosotela, the paraphysis, the velum, the dorsal sack enveloping epiphyses I and II, the supracommissure and then the epiphysis (II).

#### SUMMARY.

1. Epiphysis I (anterior epiphysial vesicle) persists in adult *Amia* and has a strong fiber connection with the left habena.

2. The cavity caudad of the velum possesses in *Amia* and *Lepidosteus* lateral extensions which extend cephalad and caudad for a considerable distance.

3. The paraphysis is present in *Amia* and *Lepidosteus* and seems a distinct structure.

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## DESCRIPTION OF FIGURES.

## ABBREVIATIONS.

<i>ch.</i> —chiasma.	<i>hb.</i> —habena.
<i>s. d.</i> —dorsal sack.	<i>hy.</i> —hypophysis.
<i>d. l.</i> —lateral diverticula.	<i>mtp.</i> —metaplexus.
<i>epi.</i> —epiphysis (epiphysis II.)	<i>par.</i> —paraphysis.
<i>epi. I.</i> —cephalic epiphysial vesicle (epiphysis I.)	<i>vel.</i> —velum transversum.
	<i>II.</i> —optic nerve.

*Fig. 1.* Transection of the Brain of *Amia* at the level of the cephalic epiphysial vesicle, showing its fiber connection with the left habena, and the lateral diverticula. The cephalic tips of the optic lobes and the connective tissue adjoining, which occupy space enclosed by the outer line are omitted to simplify the figure.

*Fig. 2.* Transection of the prosencephal of *Lepidosteus*, to show the epiphysis (II), dorsal sack, paraphysis, and the lateral diverticula of the cavity.

*Fig. 3.* Transection through the prosencephal of *Amia*, showing the epiphysis, dorsal sack, paraphysis and cephalic extensions of the diverticula.

*Fig. 4.* Transection of the brain of *Amia*, showing the same general features as figure 3, but farther caudad, at the level of the opening of the paraphysis.

*Fig. 5.* Transection of the metencephal of *Lepidosteus*, showing the lateral extension of the cavity beneath the metaplexus.

## THE EARLY DEVELOPMENT OF THE EPIPHYSIS AND PARAPHYSIS IN AMIA.

By A. C. EYCLESYMER and B. M. DAVIS.

*With Plate VII.*

Recent researches indicate that the solutions of certain problems connected with the early development of the epiphysis and paraphysis are to be approached through a study of the early history of these structures in Fishes. Thus far little has been written concerning their early development in Ganoids.

Balfour and Parker describe and figure the early stages in the development of the epiphysis in *Lepidosteus*. It arises as a single, median, posteriorly directed outgrowth from the anterior portion of the thalamencephalon. Beyond the fact that the outgrowth is at first directed backward there are no points which claim special attention.

Salensky figures an early stage of the epiphysis in *Acipenser ruthenus* as a single, median, posteriorly directed outgrowth from the roof of the thalamencephalon.

Kupffer describes and figures the early development of both the epiphysis and paraphysis in *Acipenser sturio*. The epiphysis is first defined in an embryo of about 57 days as a single, median, posteriorly directed outgrowth. The distal part of this conical evagination is soon converted into a vesicle, while its proximal portion gives rise to the stalk. The paraphysis first appears in an embryo of about 64 hours as a slight evagination in the posterior portion of the roof of the prosencephalon. It soon assumes the form of a vesicle which at the end of the larval period sends off a number of diverticula.

Hill studied certain larval stages of *Amia calva* (10-15 mm.) and described three outgrowths from the roof of the the brain. Two of these were found to arise from the roof of the thalamencephalon, but owing to lack of material the author

states that he was "unable to describe their earliest condition or give their subsequent history." The third makes its appearance in a 13 mm. larva as an evagination in the roof of the prosencephalon.

Since our sections of *Amia* show many interesting and undescribed features we have thought that the following notes taken from our manuscript on the organogeny of *Amia*, might be worthy of special mention.

Our material was fixed in chrom-osmo-acetic, picro-acetic and corrosive-acetic. Our sections comprise the embryonic and larval stages. They were prepared during the winter of 1895 by Mr. Brockett, preparateur of the Cambridge Morphological Laboratory. The senior author wishes here to express his gratitude to Mr. Adam Sedgwick and Dr. Hans Gadow for the many courtesies shown.

The literature on the epiphysis and paraphysis has been so often compiled that we deem no apology necessary for its omission.<sup>1</sup>

In order to obtain an accurate conception of the contour and relation of parts we have made reconstructions after the method described by Born.

*Embryo 3-4 days.*

The epiphysis invariably appears earlier than the paraphysis. We have usually found it present in embryos which extend over about two-thirds of the meridional circumference of the yolk. At this time the blastopore is still widely open. The secondary optic vesicles are invaginated and the lens appears as a thickening of the inner layer of the epiblast. While the epiphysis is generally present at this time we have series of the same stage in which there is no trace of it, and even in later stages when the blastopore is completely closed and the tail free

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<sup>1</sup> A complete bibliography has been published by the junior author in the *Proc. Indiana Acad. Sci.* 1897. The reader is also referred to the very excellent abstracts of the principal papers given by Sorensen in the *Journ. Comp. Neurol.* 1894, pp. 12-73.



from the yolk we have failed in a number of embryos to detect its beginning.

The epiphysis (*er*) first shows as a slight evagination in the roof of the primary fore-brain as shown in Fig. 1. The appearance of this section suggests that its beginning might have been primarily the result of an *invagination* of the brain at the point *x*; the two folds later assuming the form shown in the figure.

A transverse section of this stage (Fig. 2) shows a lateral extension of its distal portion. There is at this time little differentiation in structure. We have noticed in a number of cases that the cells forming the outer layer appear somewhat larger than the others. Aside from this we have not been able to find any histological characters which would distinguish it from the adjoining brain wall. Neither have we found in the earlier stages any peculiarities by which we could predict its point of origin.

#### *Embryo 5-6 days.*

In this stage the tail of the embryo is just becoming free from the yolk and the outline of the heart is barely visible. The epiphysis, or primary vesicle, when reconstructed, is found to be a small oblong mass of cells lying in the median line.

A sagittal section is represented in Fig. 3. It is here obvious that the vesicle (*er*) has flattened dorso-ventrally and elongated posteriorly. A distal and proximal portion may now, in a general way, be distinguished. The longer distal portion lies nearly in a horizontal plane with its ventral wall closely applied to the brain roof; this passes over into the narrow proximal portion which connects it with the brain wall. Its lumen, which was short and conical, has now extended posteriorly, widened laterally, and flattened dorso-ventrally. Its opening into the third ventricle is well shown in the section. It is also apparent that the dorsal wall of the vesicle already manifests important changes; throughout the greater portion of its extent it has undergone a decided thinning, so that it now consists of but one to two layers of cells. It is important to note that this

is not the case in the proximal portion of the dorsal wall; here is an area (*e2*) which remains thickened and is destined to play an important part in the later history of the vesicle. The ventral wall of the vesicle is from three to four layers of cells in thickness. It is noticeable that all the cells of the vesicle present, now and in subsequent stages, a somewhat different appearance from those forming the roof of the brain, in that they are less deeply stained, larger, and approach a spherical form.

A transverse section (Fig. 4) along the line 4-4 of Fig. 3 shows the dorso-ventral compression of the primary vesicle, the outline of its lumen, and the form and relative thickness of its walls.

The epithelium (*ep*) above the vesicle is but a single layer of cells, while around this area it thickens to a double layer as shown in the figure. Between the epithelium and the brain scattered mesoblastic cells are always present, except in the area just above the vesicle.

*Larva 6-7 days, 4.5 mm.*

A reconstruction of the primary vesicle in a larva at this stage is shown in Fig. 5. Viewed from above it presents posteriorly a more or less oval appearance, while anteriorly it gradually narrows as it passes over into the proximal portion which connects it with the brain wall.

A sagittal section (Fig. 6) taken along the line 6-6 of Fig. 5 shows that the vesicle has changed but little in general outline. The dorsal wall throughout the greater portion shows no changes beyond those described in the preceding stage. In the region of the proximal thickening (*e2*) there is an increased proliferation of cells. In this vicinity we can, for the first time, distinguish a slight evagination of the wall of the primary vesicle. It is important to note just here that this evagination cannot be considered as an evagination of the brain wall, but is far up on the dorsal wall of the primary vesicle. Its ventral wall shows no marked change.

A transverse section is shown in Fig. 7, its position being indicated by the lines 7-7 of Fig. 6. The general outline of

the vesicle, the form of its lumen, and the relative thickness of its walls are here further illustrated. The inner layer of the superficial epiblast immediately above the vesicle, which in the earlier stages is practically wanting, is now extending over this area. A short distance in front of the vesicle there is a small transverse fold of the brain wall; this fold extends antero-ventrally and marks the boundary between the thalamencephalon and prosencephalon.

*Larva 8-9 days, 5-6 mm.*

An examination of the living larva reveals no external peculiarities which would indicate the position of the vesicle.

A reconstruction of the vesicle at this stage closely resembles Fig. 5, except that its stalk has narrowed, and there has appeared a rounded protuberance in the proximal portion of its dorsal wall.

A median sagittal section is shown in Fig. 8. The contour of the distal portion remains the same as in the previous stage. In the dorsal wall the slight evagination referred to in the preceding stage is better defined, causing the lumen to widen at this point. It is now apparent that we are here dealing with a secondary vesicle (*e2*) formed as a diverticulum of the first. Histologically its structure is essentially the same as the adjacent wall of the primary vesicle.

*Larva 9 days, 6-7 mm.*

The living larva at this time shows pigment in the retina and head region where it is distributed quite uniformly, except in a mid-dorsal area which lies slightly anterior to the lateral eyes. This area marks the position of the underlying primary vesicle.

A reconstruction of this stage (Fig. 9) shows that the primary vesicle is more sharply defined, owing to the fact that its anterior margin has extended forward over its ventral portion; but aside from this it has undergone little change in outline. The reconstruction now plainly shows a well defined smaller vesicle (*e2*) lying anterior to the primary and delimited by a shallow groove. It lies, at first, so far as we have ob-



served, in the median line. It is slightly flattened antero-posteriorly, so that its long axis coincides with a transverse section of the head.

A sagittal section (Fig. 10) taken along the line 10-10 of Fig. 9 shows a considerable increase in the size of the primary vesicle. Its ventral wall is much thicker and its lumen narrower than in the earlier stages. The secondary vesicle appears as a mass of cells which, as yet, possesses no lumen beyond that shown in this section. Its cells appear in all essentials like those forming the primary vesicle. This section confirms the surface observations as regards the distribution of pigment (*p*). It is noteworthy that the pigment is discontinuous over the primary vesicle while it extends entirely over the secondary.

Fig. 11 represents a transverse section along the line 11-11 of Fig. 10. In this, as in the sagittal section, the lumen appears to be very narrow and is bounded above by a single row of cells. Fig. 12, taken along the line 12-12, passes through the secondary vesicle, and further illustrates its form and structure.

*Larva 10 days, 8 mm.*

The continued formation of pigment in the head region, excepting the area to which we have already referred, serves to more sharply define the position of the underlying vesicles.

The reconstruction (Fig. 13) shows that the primary vesicle (*e1*) has elongated antero-posteriorly. The secondary vesicle (*e2*) has maintained its general form but has shifted its position, as shown in the figure, so that its long axis now forms an angle of  $10^{\circ}$ - $15^{\circ}$  with the long axis of the body.

A sagittal section (Fig. 14) in the plane indicated by the line 14-14 shows, in a general way, the relation of the vesicles to the brain roof. Fig. 15 is a more highly magnified view of the vesicles. The ventral wall of the primary vesicle shows a continued increase in thickness, while the dorsal still remains unchanged. The continued expansion of the brain roof has caused an approximation of the walls of the stalk and a consequent obliteration of the cavity of the primary vesicle. The

secondary vesicle shows no histological changes beyond the condition represented in Fig. 10.

The inner layer of the epithelium (*ep*) has now extended completely over the vesicles. There is a noticeable increase in the degree of pigmentation, but as yet it has not appeared in the area over the primary vesicle.

Transverse sections of a corresponding stage are shown in Figs. 16, 18, 19. These are taken along the lines indicated by their respective numerals in Fig. 13. They show the relative size and position of the two vesicles. Fig. 17, taken along the line 17-17 of Fig. 15, represents an oblique section of the primary vesicle and possibly the continuation of its cavity within the secondary. Of this we are in doubt since we have not observed the lumen of the secondary vesicle until a much later stage. Just beneath the posterior margin of the primary vesicle there is a thickening of the brain wall. The upper layer of cells constituting this portion are elongated dorso-ventrally; their nuclei occupy the lower portions of the cells while their upper ends become granular. This tract is the beginning of the posterior commissure (*p. c.*).

While the usual conditions are as above described, we have series which show marked variations in the position of the secondary vesicle, in that it lies on the opposite side of the primary. Furthermore we have noticed that in some cases the secondary vesicle is scarcely visible and seems no further developed than in the 6 mm. stage.

*Paraphysis.* The so-called "paraphysis" is described by Hill as first appearing in a 13 mm. larva. We have found the structure well defined in the 8 mm. stage. It arises in *Amia*, as in *Amblystoma*, as an evagination of the posterior portion of the roof of the prosencephalon. Its basis is foreshadowed by a considerable thickening of the brain wall. This thickened tract consists of a single layer of columnar epithelium, the cells of which, aside from their being elongated, resemble those in the adjacent brain wall.

*Larva 14-15 days, 9-10 mm.*

The living larva from this time on usually shows, externally, no trace of the translucent area which in an earlier stage marks the position of the underlying vesicles. In some cases we have noticed it still present in the 11-12 mm. larva; its disappearance is due, as will be seen, to the formation of pigment beneath this area.

A reconstruction of this stage is shown in Fig. 20. The primary vesicle when viewed from above is much the same in general outline as in the previous stage, but when seen from the side its dorsal growth is apparent. The secondary vesicle has likewise grown, especially in length, and has shifted its position to the left and downward. Its long axis now coincides with the long axis of the body.

A sagittal section slightly magnified (Fig. 21) shows the relation of the epiphysis to the other parts of the brain. Fig. 22 represents a more highly magnified view of the same section through the vesicles. The primary vesicle is more or less oval in outline, tapering to a point at its distal end. The stalk is narrow at its base, but broadens as it merges into the distal portion. It possesses a compressed, but well defined, lumen which ventrally opens into the third ventricle; dorsally it forms the cavity of the vesicle. This cavity is bounded above by a wall two rows of cells in thickness, while the ventral wall is several rows of cells deep. It will be seen in this section that pigment has formed in the region immediately above the vesicles. At this time the superior commissure (*sc.*) is differentiated and lies in close contact with the stalk of the primary vesicle.

Figs. 23, 24, 25, 26 represent transverse sections along the lines indicated by these numerals in Fig. 20.

Fig. 24 shows a longitudinal section of the superior commissure. We have carefully studied the relation of this commissure to both vesicles, but have been unable at this stage to trace fibers into either. Fig. 25 illustrates the further differentiation of stalk and vesicle. It also shows the overgrowth of the primary over the secondary vesicle. It is noteworthy that



even at this comparatively late stage there is as yet no trace of a lumen in the secondary vesicle.

*Paraphysis.* The paraphysis has grown in length and has assumed the form of a vesicle. It extends farther forward than in the earlier stage. Histologically its walls show the same characteristics noted in the preceding stage, consisting of a single layer of thickened columnar epithelium. Its posterior wall possesses considerable pigment while its anterior and dorsal walls seem to possess little or none.

*Larva 19-20 days, 12-13 mm.*

Fig. 27 is an outline of the roof of the third ventricle showing the position and relative size of the epiphysis. Fig. 28 represents an enlarged section through the epiphysial region. When compared with the preceding stage certain changes are observed. The vesicle extends farther forward and is compressed dorso-ventrally. The superior commissure (*sc.*) has been crowded farther into the third ventricle. The roof of the third ventricle just anterior to the commissure is much thinner than in the preceding stage.

In this stage we have noticed for the first time a peculiar tract (*ft.*) lying in the ventral portion of the primary vesicle, which, from its similarity to the commissure lying immediately below, we interpret as a fiber tract. The relative positions of the vesicles are well shown in the series of transverse sections 29, 30, 31, 32 taken along the lines bearing their respective numbers in Fig. 28. Fig. 30 shows that the overgrowth of the primary over the secondary has progressed beyond the condition shown in Figs. 20, and 25 of the preceding stages. In Fig. 31 the tract (*ft.*) already noticed in the sagittal section (Fig. 28) is well defined. It lies in close contact with the superior commissure (*sc.*).

In some of our sections of this stage we have not been able to show the existence of nerve fibers passing from either the superior or posterior commissures into this tract. In one series however, we have been able to trace, beyond any shadow of doubt, nerve fibers passing directly from the superior

commissure into the stalk of the primary vesicle as shown in Fig. 33.

The secondary vesicle is much as described in the preceding stage. As yet we have not observed a well defined lumen. We have noticed, however, a condition similar to that shown in Figs. 20 and 31, where the cells are scattered, and which might be considered the forerunner of the cavity which is about to appear.

An interesting feature of this stage is the retarded formation of cartilage over the vesicles. At this time the increase in formation of pigment is not only apparent in the skin, but it likewise begins to form in the connective tissue surrounding the vesicles.

*Paraphysis.* The paraphysis has increased considerably in size; its walls still consist of a single layer of cells, the anterior being thicker than the posterior. Antero-dorsally it sends off two diverticula. The larger one extends forward in line with the paraphysis, while the smaller lies to the left and extends laterally. Histologically these diverticula do not differ from the anterior wall of the paraphysis.

*Larva 22-26 days, 15-16 mm.*

With the formation of cartilage the skull begins to take definite shape, and with these changes there arises a considerable space between the roof of the brain and the skull (Fig. 34). The effect of these changes on the form of the epiphysis is well shown in Fig. 35, which represents a more highly magnified view of the epiphysis in the plane of Fig. 34. The stalk is much longer than in any previous stage and the structure as a whole is inclined slightly forward. The upper portion, or vesicle proper, forms a continuous oval outline with the stalk. Posteriorly it extends over the stalk, and the whole structure has the general appearance of the upper portion of an interrogation point. Its lumen follows the general outline, is well defined throughout its entire extent, and is still widely open into the third ventricle.

Transverse sections of this stage are shown in Figs. 37, 38,

39, 40. The positions of the sections are indicated by their numerals in Fig. 45. The sections show that the primary vesicle is inclined toward the right. The structure as a whole has increased in size, but this is due largely to the growth of the stalk. The walls of the vesicle retain the same relative thickness as in the preceding stage. Its lumen is better defined and is apparently filled with a coagulum. The layer of cells lining the cavity of the stalk and those forming the ventral wall of the vesicle have elongated and become pear-shaped in general outline, with their smaller ends pointing inward.

The secondary vesicle has not changed its relative position. It has narrowed somewhat and appears longer dorso-ventrally. For the first time a well defined lumen is present. We have not been able to find any trace of a communication with the lumen of the primary or to find an opening into the thalamo-coele. The cells lining this cavity are likewise elongated, with their narrower ends directed inward. At one point, as shown in Fig. 39, the superior commissure is in direct contact with this vesicle, and several nerve fibers enter it, but can be traced only a short distance.

It is of interest to note that the cartilage (*c*) just above the primary vesicle is much thinner than in other portions, being hollowed out, so to speak, for the reception of its distal portion.

*Paraphysis.* The growth of the paraphysis has kept pace with other parts of the brain. It has broadened distally and the two diverticula noticed in the preceding stage are almost equal in size and project on either side, so that the whole structure becomes bilaterally symmetrical. In some sections of this stage there are indications of the formation of secondary diverticula.

*Larva 30-35 days, 22-23mm.*

Fig. 41 represents a diagram of the roof of the third ventricle. The primary vesicle is somewhat larger than in the preceding stage, but in general form it is essentially the same. It stands out less prominently owing to the fact that the cerebral hemispheres have grown up around it. It shows a contin-



ued forward movement. In the preceding stage its axis was approximately perpendicular, whereas in the present it is inclined anteriorly some  $15^{\circ}$ . Its cavity is about the same in form and extent. The walls of both stalk and vesicle remain unchanged. The elongated pear-shaped cells lining the cavity appear as shown in Fig. 39.

The secondary vesicle lies relatively lower and is more obscured, owing to the continuous overgrowth of the primary. Its form is that described in the preceding stage, while its volume is somewhat less. Its lumen, which was plainly visible in the preceding stage, is but faintly indicated and in some cases has entirely disappeared, while the elongated cells lining the early cavity are no longer distinguishable.

The cartilage which in earlier stages was noticeably thinner just above the vesicle has now become of uniform thickness in this region; the layer of pigment lying just beneath the cartilage is not yet continuous over the vesicle.

*Paraphysis.* The paraphysis has increased greatly in size; along its middle portion it appears bilobed, while distally it ends in a large median prolongation. There appear at this time numerous foldings and diverticula.

#### SUMMARY.

We confirm the observations of Hill that there are three outgrowths from the roof of the brain, two of which (primary and secondary epiphyses) arise from the roof of the thalamencephalon, while the third (paraphysis) arises from the roof of the prosencephalon.

The primary epiphysis first appears in a 3-4 days embryo as a median, posteriorly directed, unpaired evagination. It soon differentiates into a narrow stalk-like portion which proximally passes over into the brain wall, while distally it enlarges to form a vesicle. A well defined lumen extends throughout the structure and opens into the thalamocoele. The walls of the vesicular portion are at first several layers of cells thick. The dorsal wall thins to one or two layers, except in its proximal portion, where it remains thickened. The ventral wall be-

comes thickened in the earlier stages but later undergoes but little change. The cells lining both stalk and vesicle become ovate-lanceolate in the 12-16 mm. stages, and are arranged so that their pointed ends are directed inward. The lumen of both stalk and vesicle are at this time filled with a coagulum. In the 12 mm. stage we have found nerve fibres passing from the superior commissure into the stalk of the primary vesicle. In the stages between 6 and 12 mm. the position of the vesicle is externally visible owing to the retarded formation of pigment in this area. Another point of interest is the thinning of the cartilage just above the primary vesicle. The primary vesicle as it enlarges grows forward, the angle formed with the horizontal plane is at first about  $5^{\circ}$ - $10^{\circ}$ , while in its final position it forms an angle of  $45^{\circ}$ - $60^{\circ}$ .

The secondary vesicle does not form until long after the primary. It usually appears on the 7th or 8th day, yet in some cases it does not appear until the 9th day. Its beginning is a slight thickening in the anterior portion of the dorsal wall of the primary vesicle; this thickening is in the median line and is accompanied by a slight evagination of the wall of the primary vesicle. As the secondary enlarges it shifts its position to the left until the two vesicles lie side by side. It is interesting to note that this vesicle in a number of cases lies on the opposite side of the primary. A well defined cavity is present in the 15 mm. stage yet in no case have we found it well defined in the earlier stages. At this time it lies practically free from the primary. In one instance we have traced nerve fibres from the superior commissure into the basal portion of this vesicle. From the 15 mm. stage on this vesicle becomes smaller, loses its cavity and undergoes other changes which are probably indicative of degeneration. It may ultimately disappear. This must be determined by studying stages beyond the 30 mm. larvae.

The paraphysis arises later than the secondary epiphysis. Its beginning is usually foretold by a thickened area of the epithelium forming the roof of the prosencephalon which soon gives rise to a posteriorly directed evagination. The structure in-

creases rapidly in size and soon assumes the form of a pear-shaped vesicle. In the 12-13 mm. stage it sends off two large diverticula from its distal end. These in turn soon give rise to secondary diverticula and cause the structure to appear digitate in the later stages. Nerve fibres have not been observed and it is probable that the structure is non-nervous. It does not come in contact with the epiphyses up to the 30 mm. stage; beyond this we have not observed.

#### SOME GENERAL CONSIDERATIONS.

The embryologist who contemplates the study of the pineal organ soon recalls the old syllogistic statement: "The pineal organ is probably a sense organ. The sense organs are paired structures, ergo, the pineal organ should be a paired structure." The *à priori* reasons are undoubtedly cogent, and certain facts and arguments have been adduced to prove their validity. Are the facts adequate? Are the arguments convincing?

It is quite beyond the province of the present paper to to enter upon an extended review of the literature on the development of the epiphysial structures in the different classes of Vertebrata. It may not be premature, however, to glance over the evidence thus far presented in the Fishes.

A well defined parietal organ first appears in the Cyclostomes, yet there are suggestions of its forerunner in Amphioxus. We quote the following from a paper by Dr. Ayers, (*Journ. Morph.*, Vol. IV, 1890, p. 228): "After a careful study of the Amphioxus eye-spot and related structures I have become convinced that the animal presents us with the earliest stage in the phylogenetic development of the vertebrate eye." Although this pigment presents a variety of forms the author finds "The most usual form that of a slightly bilobed mass, the lobes being placed to the right and left of the median line, so as to cover the roots of the first pair of cranial nerves more or less completely." (p. 230). "For greater functional power, the central (median) portion of the pigment spot has grown upwards (dorsad) and carrying with it a portion of the ventricular wall has produced the pineal eye." (p. 241). "The pari-



et al.-pineal eye of the Cyclostomata and other vertebrates has been developed from a median portion of the pigmented eye of *Amphioxus*. The rudiments of the eye were derived from (segmental) sense organs, but the eye itself is never developed from two right and left halves, in so far as the closure of the medullary folds would necessitate this."

Petromyzon is the only form among the Cyclostomes in which the early history of the epiphysial structures has been traced. In the adult, Ahlborn discovered two epiphysial vesicles, and from their position called them the superior and inferior. Dohrn, Balfour, Scott, Owsiannikow and others showed that the superior arises at about the time of hatching (3.4 mm. larva) as an evagination of the roof of the thalamencephalon. These investigators found that the inferior vesicle did not appear until the larva had reached a very late stage (17-26 mm.). Whether the inferior vesicle was an outgrowth from the superior, or arose from an independent source was not known until Kupffer clearly showed its mode of origin. The author found the superior to arise at the time and in the manner described by the above named investigators. The inferior however arises in a 5 mm. larva as an evagination in the posterior portion of the roof of the prosencephalon. This structure grows backward and its distal end enlarges to form the inferior vesicle of Ahlborn. To this structure Kupffer gives the name "second epiphysis" and believes it to be directly homologous with the paraphysis of *Amphibia*.

Studnicka, in a publication prior to that of Kupffer, found the superior to arise as described by previous authors. He described certain stages in the development of the "parapineal organ" ("inferior vesicle", "second epiphysis") and believes, although he did not observe the early stages of development, that this organ arises from the roof of the thalamencephalon in front of the superior commissure and not from the prosencephalon as stated by Kupffer. Studnicka maintains that there is a third outgrowth from the roof of the prosencephalon which corresponds to the paraphysis of other forms.

According to all authorities these two organs are highly nervous. Studnicka found the superior vesicle to be attached to

the left ganglion habenula and likewise attached to the right habena at two points. The inferior vesicle is at first, according to both Studnicka and Kupffer, in connection with both the right and left ganglia habenulae. The union with the right is soon severed while that with the left remains.

While the question of innervation needs further investigation, the early history of the vesicles would seemingly preclude all possibility of their being considered as right and left mates. Of course it is possible that each may represent one or several pairs of fused sensory *Anlagen*, but until some evidence is forthcoming this is merest conjecture.

In 1892 (*Anat. Anz.*, Vol. VII, p. 217) the senior author called attention to a remarkably early differentiation of the bases of the optic vesicles in *Amblystoma* and *Rana* in the following words: "I believe I have proved in *Amblystoma* and *Rana*, that the lateral eyes are present as a pair of depressions in the cephalic neural plate." \* \* \* "I hope to establish, beyond question, that they are present as distinctly differentiated areas at the time the medullary groove first appears." In a second paper (*Jour. Morph.* Vol. VIII, pp. 189-94) evidence was adduced which seemed to demonstrate the validity of the above statements.

In 1893 Professor Locy gave notes upon the appearance of like structures in the unclosed neural plate of *Squalus acanthias*. In addition to these, other depressions were found which the author called "accessory optic vesicles." The conclusions drawn from these observations are here given in the words of the author: "There are preserved on the cephalic plate of Elasmobranchs (*Squalus acanthias*) at least two pairs of accessory optic vesicles.

These taken with the primary optic vesicles, give to the embryo three pairs of rudimentary eyes."

If these observations are correct, we have, as the author states, "a multiple eyed condition in the embryos of these animals. This is common enough in the invertebrates, but has not been previously noticed in Vertebrates." The rejuvenation of an hypothesis which for a score of years has been continu-

ally ringing in the ears of the more ardent phylogenists will be hailed with delight.

Since the observations of Professor Locy are of such great theoretical import it may not be out of place to review them somewhat in detail. If we interpret correctly the text and figures given by the author in his various articles, we might summarize the evidence gathered from surface study as follows: The accessory optic vesicles do not appear in all embryos. Their number is far from constant (see Figs. 9 and 16, Pl. XXVI, *Jour. Morph.*, Vol. XI, which represent embryos of the same age). Their time of appearance is extremely variable, as shown by Figs. 5, 6, 8, 9, 10. They may appear as unpaired structures as well as paired, as shown in Figs. 5, 9, 10.

The above facts taken collectively form an argument which cannot be overlooked. They certainly indicate that one must be extremely cautious in the interpretation of the so called "accessory optic vesicles."

It may be opportune to mention that while studying the paired depressions in the above named *Amphibia* the senior author frequently noticed other depressions in both the neural plate and folds; since they appeared at different stages, and were neither uniform in size or depth, nor constant in number or position, they were regarded as artifacts.

In view of the uncertainty of the meaning of these depressions, when based upon surface study alone, one naturally seeks for further evidence in their histological structure. This Professor Locy sums up in his final paper as follows: "My sections are not favorable for a critical study of the histological conditions, but it is clear, from them, that a differentiation starts in the anterior patches similar to that mentioned above, for the true eye vesicles. There is a greater frequency of dividing cells and many of the cells become elongated and pear-shaped."

If we turn to the description of the true eye vesicles, we read: "Sections of the earliest-formed circular areas, show something in the direction of histological differentiation. Mitoses are more frequent and more of the cells are elongated and



pear-shaped than in the other parts of the cephalic plate. The differentiation is by no means as marked as in the *Rana palustris* figured by Eycleshymer—nevertheless indications of change are not only wholly lacking. My sections are too thick ( $10\mu$  to  $15\mu$ ) for satisfactory histological study, but one can see in them that the middle of the walls of the optic cups are areas of differentiation. The differentiation does not progress far until later, but the frequency of dividing cells, and their change of form continue, in these early stages, to be marks for distinguishing visual epithelium from that of the surrounding brain-walls. The dividing cells are neuroblasts, and these are known to be points from which the nerve-fibers spring; their presence in any considerable number would therefore indicate a differentiation in the direction of increase of sensibility."

The elongation of cells in these areas would certainly be indicative of differentiation, providing mechanical stresses be excluded. The existence of mitotic figures in a rapidly growing structure, such as the beginning of the infundibulum in which the optic vesicles are at first located, or in the rapidly expanding walls of the thalamencephalon in which the first pair of accessory vesicles are incorporated, would not necessarily indicate a differentiation in the direction of increase of sensibility. That the epithelium is "visual" would also appear questionable.

It can be said with perfect certainty that even where the optic cups are as well differentiated as in *Rana palustris*, one cannot by any known method demonstrate the "visual character" of the epithelium. During the involution of the optic cups, as the senior author stated in an earlier paper, "a marked migration of the pigment has taken place: instead of being located at the ends of the cells, as in the earlier stages, it is found between them and nearer the periphery. The nuclei have likewise undergone a further migration toward the surface, so that the cells of the superficial layer have completely lost their identity." Their fate is unknown.

Should later investigation prove that in the unclosed neural plate of *Squalus* there are present from two to eight pairs of

rudimentary eyes another question arises, viz: Is there sufficient evidence to show that two of these unite to form the pineal outgrowth?

Concerning the fate of the anterior pair we read the following in Prof. Locy's earlier paper (*Anat. Anz.*, 1893, p. 173):

"I have been able to follow the anterior pair, step by step through a graded series of embryos, without having once lost trace of them, and to see that they enter the thalamencephalon and give rise to the pineal outgrowth. The posterior pair, which are smaller, are not to be followed in this definite way, they become fainter and, I believe, they fade away."

Further, p. 174. "The accessory optic vesicles may, from certain marks that remain fairly constant, be identified with certainty both at this stage, and in later stages" \* \* "The auditory vesicle, in the process of sinking below the surface, is shifted backwards, and finally, there comes to be five of these elevations in front of it (Fig. 5 n<sup>6</sup> to n<sup>10</sup>) and, also, in the meantime, mid-brain and cerebellum have appeared. But all these transformations go so clearly that no confusion need arise if one has a suitable series of embryos."

In the final paper certain statements are found which lead one to infer that the fate of even the first pair of vesicles may perhaps be regarded as somewhat problematic, viz:

"The bulging of the walls to form the mid-brain vesicle has come on insiduously, and has taken a position behind the vesicles of the paired eyes, in apparently the same position previously occupied by the accessory vesicles. These transformations are confusing, as the walls of the mid-brain resemble the accessory optic vesicles grown larger. In an earlier published paper I made the mistake of identifying the mid-brain with the accessory optic vesicles; but it was merely an error of identification, and did not effect the main contention of that article."

In the former paper p. 178, the author states:—"We have two pairs of these embryonic organs, in addition to the lateral eyes, and we have thus actually present, in this animal the material to supply two distinct outgrowths both visual in charac-

ter." Again p. 179, "It will be in harmony with these observations to account for two distinct structures, when they occur, by reference to this known case of the existence of two pairs of accessory optic vesicles, in front of the mid-brain region, on the cephalic plate of *Squalus acanthias*. Whether or not similar *Anlagen* for epiphysis and pineal eye exist clearly defined in other animals, can be determined only after renewed observation upon them."

In the final paper we read: "I have not been able to determine whether it is the epithelium of the first pair of accessory vesicles only, or whether epithelium from the second pair is also included. Either the epithelium of the two pairs is incorporated into the walls of the thalamencephalon by being carried together, or the epithelium of the second pair fades into the surrounding substance of the brain wall, which almost immediately grows into the vesicle of the mid-brain."

It would thus seem that the fate of the second pair of accessory vesicles is likewise unsettled.

When all these questions are satisfactorily settled in accord with the author's views, there remain serious obstacles to the homologies offered. Ritter has called attention to some of these in the following words:

"Let it be fully established that the ancestral vertebrate possessed two or more pairs of serially homologous eyes situated on the dorsal side of the central nerve axis, and we should have a good starting point for an explanation, not only of the epiphysis and pineal eye, but also of certain structures found associated with them. (The accessory structures, which it may be anticipated will find their explanation in this direction, are 1) some of the collateral evaginations from the roof of the developing brains of several groups of vertebrates; 2) the parapineal organ present in *Petromyzon*, and in some lizards, as the young of *Anguis fragilis* (Prenant, '93); 3) as a reversion the parapineal organ in an occasional adult individual of *Phrynosoma coronata*.) It must be recognized, however, that as our knowledge now stands there are some rather serious difficulties to be overcome before the explanation will be complete. With



reference to the accessory evagination, the paraphysis of Selenka, the anterior epiphysis of Eycleshymer, the endyma of Hoffmann, all are in front of the epiphysis proper, while in *Squalus*, according to Locy, it is the pair of eye cups behind the ones that develop into the epiphysis that is wholly lost by degeneration. Of course it does not necessarily follow that because the first pair behind the lateral eyes becomes the epiphysis in *Selacheans* the same would be true in *Teleosts*, where we know (Hill, '91) that an anterior secondary evagination forms and has a transient existence; nor in *Amphibians* where the same thing takes places (Eycleshymer, '92).

In *Lacertilia* the difficulty is made still greater by the fact that the secondary evaginations are not only in front of the epiphysis but also that in some species (Leydig '91) there is more than one." From the evidence thus far adduced it would seem appropriate to conclude in the words of Ritter: "Our knowledge of the whole subject is so fragmentary that generalizations based upon it and made in the light of Locy's interesting observation, must be very unsatisfactory. One of this author's conclusions is that the epiphysis is homologous with the lateral eyes. But in connection with this conclusion he remarks parenthetically that its "differences in structure need to be explained." This remark is timely and may well be extended to numerous other difficulties involved in the subject."

Before we can explain the condition observed in certain *Reptilia* (Leydig) we must either find several pairs of "accessory optic vesicles" lying in front of Locy's first pair, or explain how several pairs of those lying behind have come to lie in front. This done the next thing will be the explanation of how the anterior pair of the entire series came to give rise to a pair of widely separated lateral eyes; one or more succeeding pairs became rudimentary; how the next in order coalesced to form a median eye; and the remainder degenerated.

Concerning the early development of the epiphysial structures in *Teleosts* we knew practically nothing until the publication of Hill's observations on certain *Teleosts* and *Amia*. Hill

demonstrated beyond question the existence of two epiphysial outgrowths in *Coregonus*, *Salmo*, *Catostomus*, *Stizostedion*, *Lepomis* and likewise in the *Ganoid*, *Amia*.

In three of these forms (*Catostomus*, *Stizostedion*, *Lepomis*) single stages as observed in the living larvae are described. The remaining forms were studied in serial sections. In a single form (*Coregonus*) the author describes the origin of the two vesicles. They are here found to "arise as separate outgrowths from the roof of the brain" . . . "the opening of the anterior vesicle is a little more in front of the opening of the posterior than to the left of it."

In *Salmo*, the form most carefully studied and on which the greatest emphasis is laid, the author did not observe the origin of either the posterior or anterior vesicle. The earliest condition studied in sections is one in which "the two vesicles are attached to the brain-roof by a common stalk." "These vesicles may have been formed in any one of three ways: (1) They may be thought of as independent and separate outgrowths which have subsequently come to be borne on a common evagination of the brain roof; (2) it is possible to think of them as formed by the division of an originally single vesicle; (3) it is possible to think of the anterior as formed by constriction from the posterior." The author explicitly states that he has not obtained satisfactory sections of stages younger than that above described and "if one judges by this figure alone there is little to choose between the three methods of origin mentioned above." There is one observation recorded by Hill which deserves special mention. In a living embryo 37 days old the author found two distinct elevations of the outer surface and "beneath each of these was a slit-like lumen leading from the brain cavity toward the outer surface of the brain wall. These lumina are entirely separate from one another." The author further states that: "unfortunately this observation was made on but one living individual and, owing probably to the rapidity with which the stage is passed through, I was unable to verify it on others." The fact that the author was unable to confirm the observation on other larvae coupled with the unsat-

isfactory nature of the figure (Fig. 3a) in which the lumina might well be interpreted as mere folds in the brain wall, render the evidence on this point extremely unconvincing, moreover the usual condition observed by the author in *Salmo* is that shown in Fig. 4.

Again, the disposition of the two vesicles in *Catostomus* and *Stizostedion* as shown in Figs. 5 and 8 certainly accords with the view that the anterior is derived from the posterior.

Hill states that "*The only reason for regarding the anterior vesicle as formed at the expense of the distal end of the posterior vesicle is that it is smaller, and, aside from this single fact, one might with equal force consider the posterior vesicle as formed at the expense of the anterior.*" Since Hill does not in the present paper describe the origin of either vesicle in a single form it is evident that he has in mind a condition in which the vesicles are both well established. The above statement when applied to such a stage is undoubtedly correct, but if we turn to Hill's description of *Coregonus* as given in an earlier paper we read: "The posterior vesicle appeared about two days before the anterior."

Our observations on *Amia* show that the posterior is well differentiated long before the anterior appears. These facts would seem to show that in these forms the anterior could not be considered as giving rise to the posterior, and we venture to predict that when the earlier development is made known in the other forms studied by Hill the time relations existing will necessitate a revision of the above statement for these forms as well.

"If we regard the position in *Salmo* as the primitive one, some shifting must have taken place in the other forms. In this shifting the determining factor appears to have been the degree of development of the vesicles. Thus the relatively large size of the anterior vesicle of *Lacertilia*, due to its former functional importance, may have brought it into the median plane, because there was room for it only in that position. The epiphysis in *Lacertilia* may have come to lie in the median plane for the same reason. In Teleosts on the other hand, the epiphysis alone becomes of considerable size, and the small an-



terior vesicle finds abundant room in its primitive position at the side of the stalk of the epiphysis. It is only in the early stages in Teleosts, when the two vesicles are large relatively to the brain and are nearly of a size, that crowding causes a partial displacement of both vesicles into the median plane."

A more plausible explanation, based upon the facts thus far presented in both Teleosts and *Amia*, is that the anterior is derived from the posterior and lies primitively in the median plane, but as a direct result of the enlargement and forward movement of the posterior it is crowded out of this plane and comes to lie at the side of the posterior.

The entire evidence thus far presented in *Amphioxus*, *Petromyzon*, *Elasmobranchs*, *Teleosts* and *Ganoids* indicates that, although we have made great strides to show that the epiphysial outgrowths are derived from segmental sense organs, we have actually accomplished but little of the journey and we find ourselves in the attitude of awaiting further research.

ABBREVIATIONS.

<i>c.</i> —Cartilage.	<i>p.</i> —Pigment.
<i>e1.</i> —Primary epiphysial vesicle.	<i>pc.</i> —Posterior commissure.
<i>e2.</i> —Secondary epiphysial vesicle.	<i>r.</i> —Roof of thalamencephalon.
<i>ep.</i> —Epithelium.	<i>sc.</i> —Superior commissure.
<i>ft.</i> —Fibre tract.	<i>th.</i> —Thalamocoele.
<i>nf.</i> —Nerve fibre.	

EXPLANATION OF FIGURES.

PLATE VII.

*Fig. 1.* Sagittal section through the epiphysial fold of an embryo which extends over about two-thirds of the meridional circumference of the egg. x 160.

*Fig. 2.* Transverse section of the same stage x 160.

*Fig. 3.* Sagittal section through the epiphysial or primary vesicle at the stage when the tail of the embryo is first free from the yolk. x 160.

*Fig. 4.* Transverse section of same stage along the line 4-4 of Fig. 3. x 160.

*Fig. 5.* Reconstruction of primary vesicle of larva 6-7 days old. (4.5 mm). x 50.

*Fig. 6.* Sagittal section of the same stage along the line 6-6 of Fig. 5. x 160.

*Fig. 7.* Transverse section of same stage along the line 7-7 of Fig. 6. x 160.

*Fig. 8.* Sagittal section of primary vesicle of larva 8-9 days old (5.6 mm). x 160.

*Fig. 9.* Reconstruction of primary and secondary vesicles of larva 9 days old (6.7 mm). x 50.

*Fig. 10.* Sagittal section of same stage taken along the line 10-10 of Fig. 9. x 160.

*Fig. 11.* Transverse section of same stage along the line 11-11 of Fig. 10. x 160.

*Fig. 12.* Transverse section of same stage through the secondary vesicle along the line 12-12 of Fig. 10. x 160.

*Fig. 13.* Reconstruction of primary and secondary vesicles of larva 10 days old (7.8 mm.) showing shifting of secondary vesicle to the left. x 50.

*Fig. 14.* Sagittal section of the roof of the thalamencephalon through the epiphysial region along the line 14-14 of Fig. 13. x 15.

*Fig. 15.* Sagittal section of the epiphysial region of Fig. 14. x 160.

*Fig. 16.* Transverse section of same stage along the line 16-16 of Fig. 13. x 160.

*Fig. 17.* Transverse section of same stage taken obliquely along the line 17-17 of Fig. 15. x 160.

*Figs. 18 and 19.* Transverse sections of the same stage taken along the lines indicated by their numerals in Fig. 13. x 160.

*Fig. 20.* Reconstruction of primary and secondary vesicles of larva 14-15 days old, (9-10 mm.) showing further shifting of the secondary vesicle. x 50.

*Fig. 21.* Sagittal section of the roof of the thalamencephalon through the epiphysial region of the same stage. x 15.

*Fig. 22.* Sagittal section of the epiphysial region of Fig. 21. x 125.

*Figs. 23, 24, 25, 26.* Transverse sections of same stage taken along the lines indicated by their numerals in Fig. 20. x 125.

*Fig. 27.* Sagittal section of the roof of the thalamencephalon through the epiphysial region along median line in larva 19-20 days old, (12-13 mm.) x 15.

*Fig. 28.* Sagittal section of the epiphysial region of Fig. 27. x 125.

*Figs. 29, 30, 31, 32.* Transverse sections of same stage along the lines indicated by their numerals in Fig. 28. x 160.

*Fig. 33.* Transverse section of same stage showing nerve fibers passing from the superior commissure to the primary vesicle. x 160.

*Fig. 34.* Sagittal section of the roof of the thalamencephalon through the epiphysial region along median line in larva 22-26 days old (15-16 mm). x 15.

*Fig. 35.* Sagittal section of the epiphysial region of Fig. 34. x 125.

*Fig. 36.* Sagittal section of the secondary vesicle of the same series as Fig. 35. x 125.

*Figs. 37, 38, 39, 40.* Transverse sections along the lines indicated by their numerals in Fig. 35. x 125.

*Fig. 41.* Sagittal section of the roof of the thalamencephalon through the epiphysial region along median line in larva 30-35 days old, (22-23 mm). x 15.



## EDITORIAL.

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### THE ETHICS OF CRITICISM.

Of all the functions of editorial work that of the reviewer demands most care and conscientious attention, while it is so generally slighted as to have ceased to command respect or confidence.

A few general principles would seem to be self-evident, which nevertheless may be worth formulating afresh.

1. The writer of a scientific paper may reasonably be supposed to be actuated primarily by a desire for the advancement of his science and his effort should receive recognition at least to that extent.

2. The writer should be assumed to be a gentleman and should be treated as such until he has notoriously forfeited his claim to be so considered.

3. The mistakes or oversights for which the writer is responsible must be considered unintentional until avowed by him.

4. Criticism should emphasize the commendable features of a writer's work if any exist.

5. Personalities are utterly and absolutely out of the question in scientific reviewing.

6. A review may avoid all critical intent by confining itself to an abstract but such abstract must then be adequate and not misleading unless it be explicitly stated that only one aspect of the paper is included. The art of making a clear and competent abstract is, like that of translation, very difficult and success is rare and meritorious.

7. When a review is at the same time a critique the criticism must be explicit or where in general terms must contain illustrations of the faults pointed out.

A general statement such as "The paper displays a painful lack of discrimination" is only permissible when accompanied by instances of such failure to discriminate. A charge that "the author has failed to avail himself of the literature of his subject" should point out some omissions of the sort described. In a word, a critique must not appear to exist for the sake of finding fault but for the sake of correcting or refuting error and must be absolutely impersonal. Even such a statement as "the evidence for the author's position seems to be insufficient," harmless as it seems, were best either omitted or followed by an explanation of the ambiguity or insufficiency. If an author be charged with failure to make his point it is but just that he should be shown where and how he has erred.

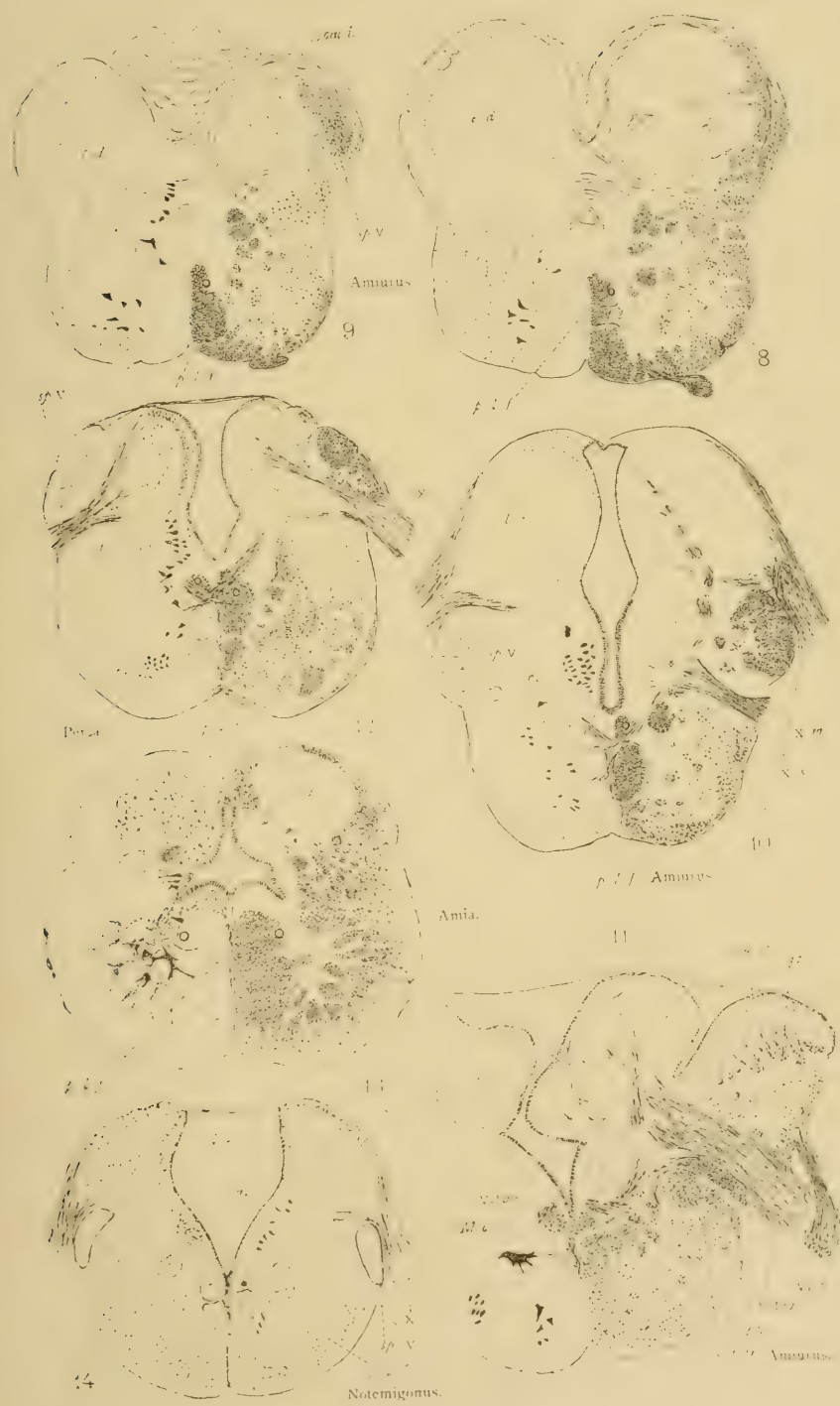
8. It ought not to be necessary to insist that the reviewer should be held responsible for a faithful effort to understand his author. The author may be obscure but before he can be taxed with this fault the reviewer must make a reasonable effort to reach his point of view. Many long and profitless public discussions would have been prevented by a private correspondence and such a course is to be recommended where at all possible. The use of the pages of a scientific periodical for purposes which could better be served by personal enquiry is to be deprecated. It is not claimed that the writer has lived up to the principles here laid down but in so far as he has failed he expresses contrition and only adds that, in order to attain the ends above sought and to add dignity to the reviewer's position, it is believed that all extended critiques should be signed by the writer.

C. L. HERRICK.

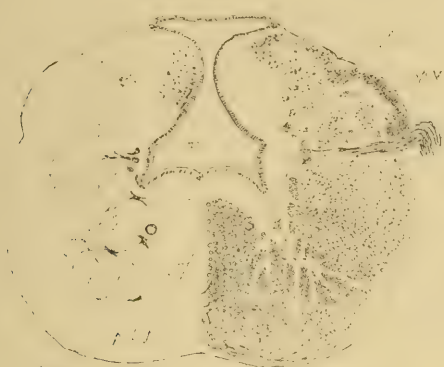






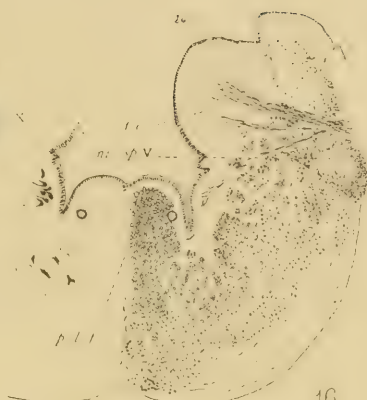






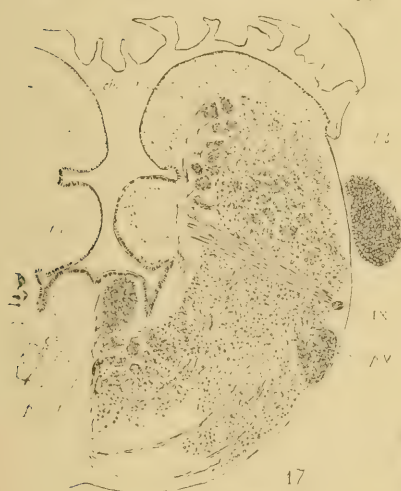
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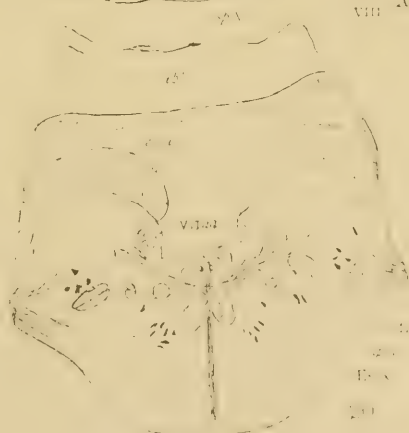


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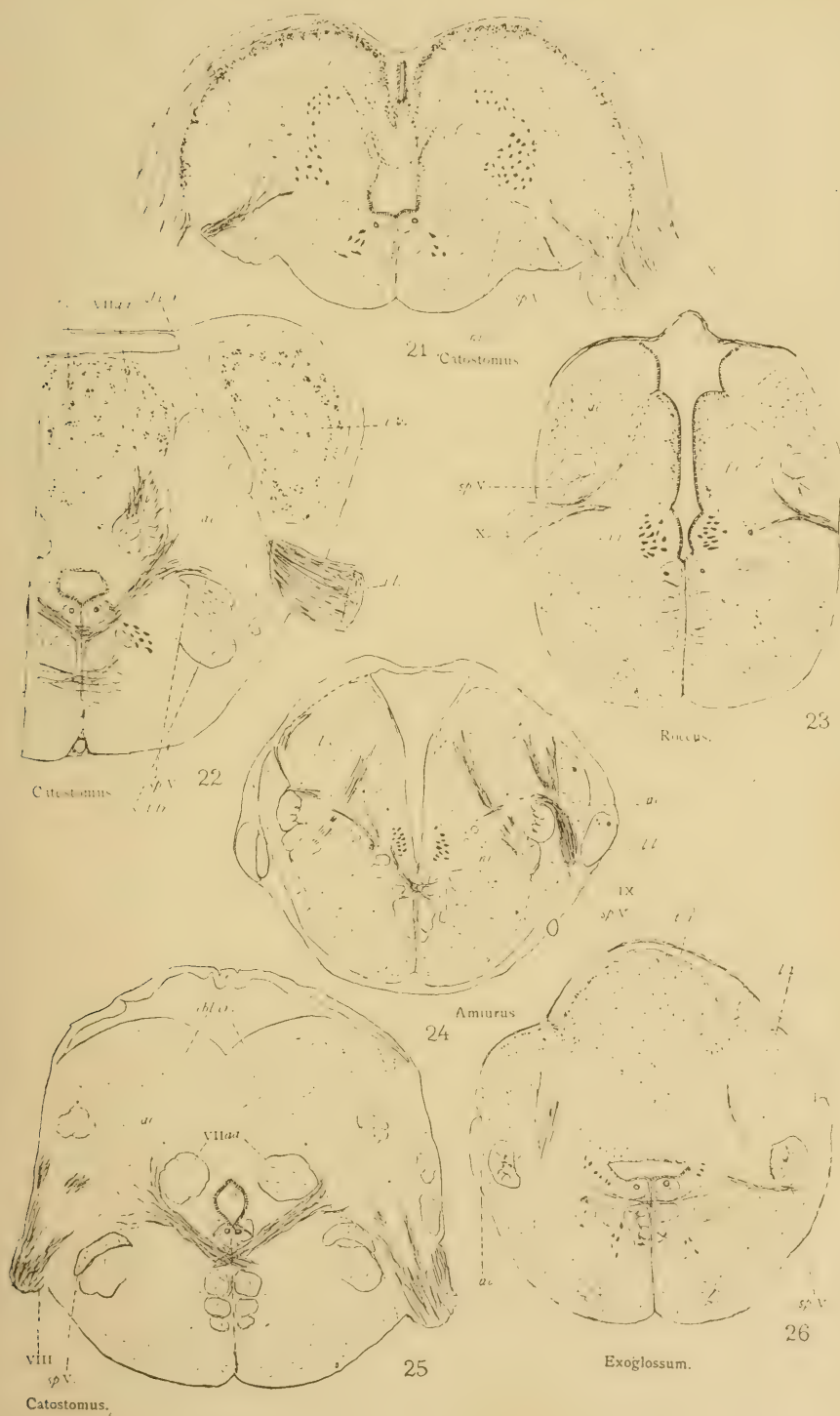
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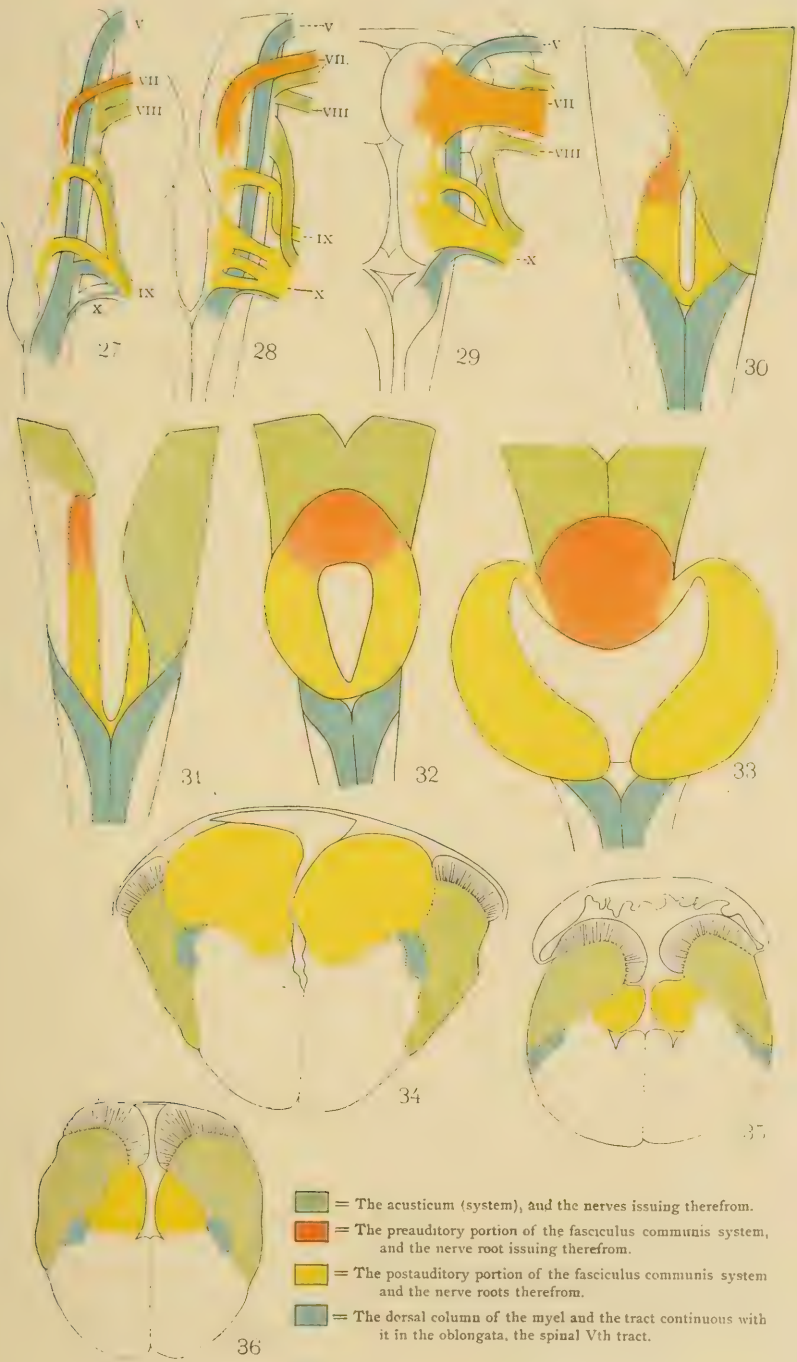
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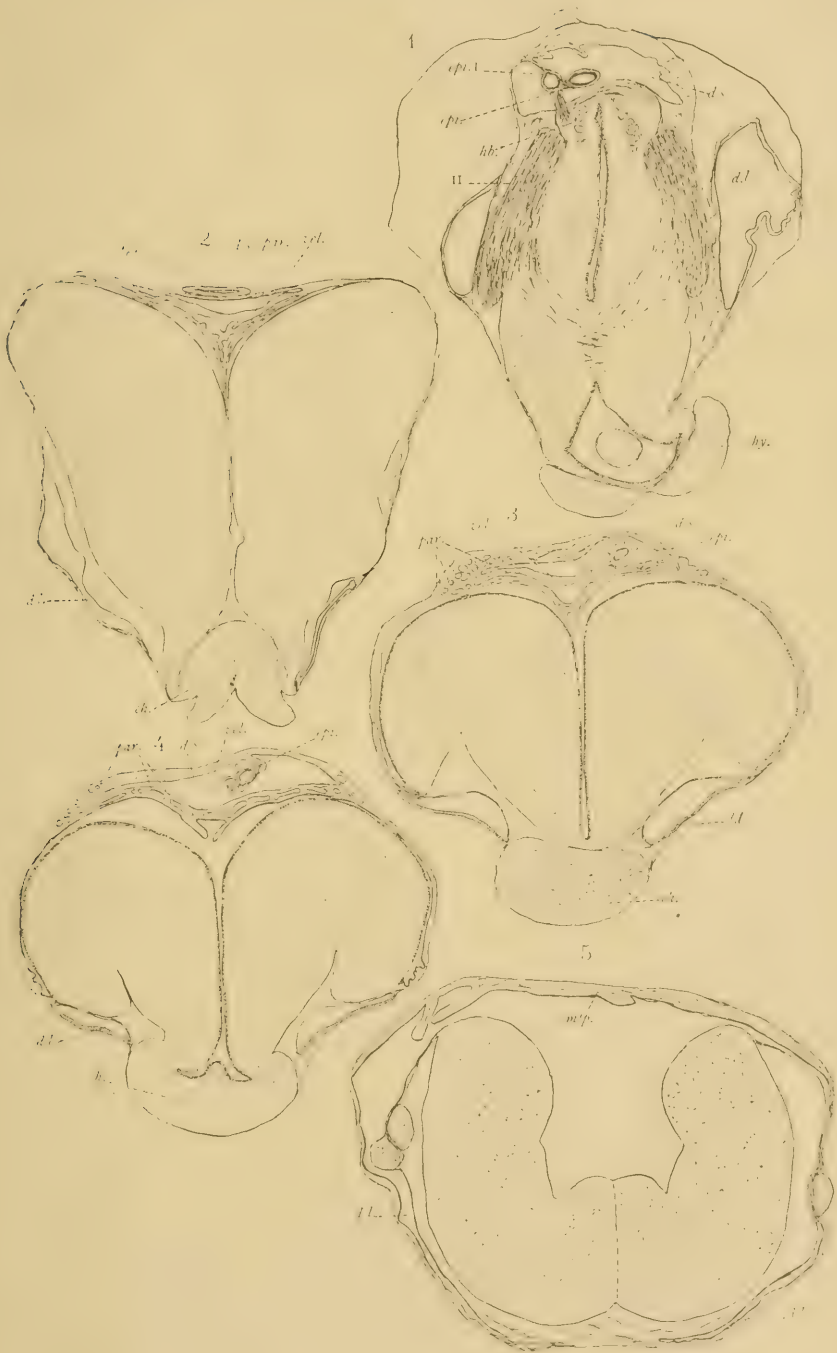




















## LECTURES ON THE SYMPATHETIC NERVOUS SYSTEM.<sup>1</sup>

By G. CARL HUBER, M. D.

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The term *sympathetic nervous system* is applied to a series of ganglia, united by intervening nerves, found on either side of the vertebral column, and extending from its cephalic to its caudal end. These ganglia with their uniting nerves form the two *great gangliated cords* or *chains*, and as such are found among all vertebrate classes, with the possible exception of some of the lowest fishes. For purposes of description, these cords are divided into a cervical, dorsal, lumbar and sacral portion, the number of ganglia in each division corresponding in the main with the number of vertebræ found in each of the above named regions; with this proviso that in the cervical region the number of ganglia is often found reduced to three. The sympathetic system includes further a number of so-called *cranial ganglia*, namely the sphenopalatine, the otic, ciliary, sublingual and submaxillary, all of which are paired, and three unpaired ganglia or aggregations of ganglia, found in the median line, in front of the spinal column. Of these, the *cardiac* is found in the thorax, the *semilunar* in the abdomen and the *hypogastric* in the pelvis. The sympathetic system comprises, further, myriads of smaller ganglia, the greater number of which are not to be seen with the naked eye. These are found in the coats of the intestine, the walls of the trachea and bronchi, in the heart and probably in or near all the larger glands of the body. From all these widely distributed ganglia, smaller or larger nerves, composed of a varying number of so-called sympathetic nerve fibers, have their origin.

Characteristic of this system is, that these nerves are

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<sup>1</sup> Being four special lectures delivered to the Medical Students of the University of Michigan in May, 1897.

united into intricate plexuses, from which arise numerous smaller branches, destined to innervate all involuntary muscle, heart muscle, the viscera and the glands.

The great majority of all the sympathetic ganglia, those of the gangliated cords, the prevertebral and perhaps also the terminal ganglia, are connected with the cerebro-spinal system through medullated nerve fibers, which leave the medulla or cord through its anterior or motor roots, and end in the ganglia. These medullated nerves constitute the so-called *white rami communicantes* of the sympathetic ganglia. Many of the sympathetic ganglia, notably those of the gangliated cords, are further connected with the spinal nerves, by means of *grey rami communicantes*. The grey rami are composed of fibers that have their origin in the ganglia, which they leave to join said spinal nerves.

This portion of the nervous system has been variously named by authors. "The older anatomists described it under the name of the *great intercostal nerve*. The fact of its being chiefly distributed to the viscera belonging to the circulatory, the digestive and generative systems led Chaussier to give it the term *tri-splanchnic nerve*, and under the supposition that it alone influenced the organic processes it was termed by Bichat the *nervous system of organic life*. The term sympathetic system, or great sympathetic, was given it by Winslow from its being believed to be the channel through which are affected the different sympathies sometimes found to exist between distant organs when in morbid condition". [7]\* And this term, although not so well chosen is now almost universally used.

A subject of frequent debate among earlier writers was, whether the sympathetic system was to be looked upon as an independent nervous system or as dependent on the cerebro-spinal system. Bichat(2), Reil, Bidder and Volkmann maintained it was functionally and structurally distinct, while Valentine and his followers denied its independence and described it as a modified cerebro-spinal nerve. The many questions involved in these discussions could however receive no definite answers

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\*The numbers enclosed in brackets refer to the literary references at the end of article.

until more was known concerning the structural elements constituting this system. The fact that the sympathetic is made up of nerve cells and nerve fibers, as is the brain and cord, was known to these earlier writers. That its nerves seemed structurally different was also known. Yet their views concerning the relation of sympathetic nerve fibers to the sympathetic cells, the endings of these fibers in the tissues to which they had been traced, and the relation of sympathetic cells and fibers to the cerebro-spinal system, were based on opinions obtained only in part by observation, speculation often playing an important rôle. This of course is not at all surprising when we consider the imperfect histological methods known to these pioneer investigators, for it must be remembered that it is only a little more than three decades since Gerlach discovered that solutions of carmine would stain effectively animal tissues.

Our knowledge of the ultimate structure of the nervous system taken as a whole has in the last twenty years been greatly extended by the results obtained through the application of new and improved methods of microscopical technique. It is however not my purpose to mention even briefly all the neurological methods which have thus materially aided in the furtherance of our knowledge. I deem it profitable however to draw your attention to two methods, consequent upon the application of which, more than upon all other methods, has the elucidation of the difficult problem here involved been possible. One of these methods was suggested by Golgi (3) in 1875, who found that nerve tissues prefixed in a solution of bichromate of potash and after-treated with silver nitrate, would take a most delicate stain, the nerve cells with all their branches, even to their finest details being most clearly portrayed. This method has become especially valuable since Ramon y Cajal has demonstrated that it is especially applicable to embryonic tissues, even in the very early stages of the developing embryo, where the structural appearances are often somewhat simpler and more amenable to a correct interpretation. The other method, of more recent origin, was suggested by Ehrlich (4) in 1886. Ehrlich found that by injecting a solution of methylen-



blue, prepared with normal salt solution, into the circulation of a living animal, many of the nerve cells and nerve fibers would be colored blue in a most satisfactory manner. The great drawback to this method as introduced by Ehrlich was that tissues so stained could be examined only in their fresh state, and even then would soon fade.

This method was however soon improved by Smirnow (5) and Dogiel (6) who showed that the tissues so stained might be fixed in a saturated watery solution of ammonium picrate, and it was further modified by Bethe (7) who found that ammonium molybdate would convert the very unstable methylen-blue stain into one practically insoluble in water and alcohol. So that tissues stained *intra vitam*, with a methylen-blue solution, may now be embedded and sectioned and even double stained without losing much of their original blue color. By way of parenthesis I may here say that, while both of these methods are applicable to the study of the entire nervous system, the Golgi method has been most useful in the study of the central nervous system, while the methylen-blue method is now more generally used in the study of peripheral ganglia, peripheral nerves and their endings.

The results obtained by these methods are so convincing that we are not surprised to find that all parts of the nervous system have been subjected to repeated investigations, since their introduction. Some of the more important results which these investigations have brought to light, are, on account of their bearing on the subject under discussion, worthy of brief mention in these introductory remarks.

As a result of these investigations we know that the entire nervous system, peripheral as well as central, is like all other tissues of the body built up of anatomical units, which, though they vary greatly in shape and size, are nevertheless to be regarded as highly differentiated cells.

Such nerve units consist of a cell body and nucleus and one or several processes. These processes are of two kinds. The one kind essential to each cell, usually becomes the axis-cylinder of a nerve fiber, and as such may attain great length,

giving off only a few branches (*collateral branches*) in its course, and terminating in a complex of end branches,—the *end-brush*. Such branches are described as axis-cylinder processes or *neur-axes*. The other kind of processes, not so essential, as many cells do not possess them, are the protoplasmic branches or *dendrites*. The dendrites may be said to be of two distinct types,—in the one, belonging to cells of sensory ganglia, the single dendrite present may also attain great length, become the axis-cylinder of a nerve fiber, and also terminate in an end-brush; in the other type, the dendrite or the dendrites break up near the cell body into secondary and tertiary branches and so on, also ending free. To such nerve units, consisting of cell body and nucleus, of neuraxis and its end-brush, and of dendrites, if present, the term *neuron* has been applied by Waldeyer. Every neuron therefore is a distinct anatomical unit, a distinct structural element, as much so as an epithelial cell, or any other cell. This *neuron-conception* of the structure of the nervous system is applicable to all its parts, to the brain and cord and all peripheral ganglia; and has been a most potent factor in the development of our knowledge of the finer anatomy of the nervous system.

Recent investigations have further shown that while a neuron is a distinct anatomical unit, it is always found associated with other neurons. Nowhere in the body of a vertebrate does one find a neuron completely disconnected from other neurons, or as Donaldson (8) has expressed it: "A group of nerve cells completely disconnected from other nerve tissues of the body, as muscle or glands are disconnected, would be without physiological significance." This association of one neuron with another is brought about by the close contiguity always existing between the *end-brush* of the neuraxis (or the end-brush of one of its collateral branches) of one neuron, and the *cell body* or *dendrite* of one or several other neurons. Investigations with Golgi and methylen-blue methods have shown that the neuraxis of one neuron may, with its end-brush, surround the cell body of another neuron by the formation of what is known as an *end-basket*; or the end ramifications of the neu-

raxis of a neuron may come in very close proximity to the end branches of the dendrites of one or several other neurons. By this contiguity of end-brush and cell body or end-brush and dendrites, neurons, while not losing their identity, are linked into chains, so that a physiological continuity exists between them. Such *nerve-chains*, or *neuron-chains*, as we may call them, vary greatly in complexity, and in the number of neurons which enter into their construction. They may be very simple, consisting of only two neurons, or very complex indeed, embracing a large number of them.

The entire nervous system may therefore be said to be made up of such neuron chains, and the tracing of them is a problem, which, perhaps more than any other, engages the attention of the neurologist at the present time. For it is only as the respective positions of the several links in such chains or paths become established, that the results of the many investigations become of practical value.

It may be seen from what has been said, that the cells of the peripheral ganglia, the various sympathetic ganglia included, the peripheral nerves, as well as the neurons in the central nervous system, form each in its respective place, a link or a portion of a link in such a chain. These neuron-chains are paths along which nerve impulses travel from the periphery to the nerve centers; from one nerve center to another; and from the centers to the peripheral tissues, such as muscles, glands, etc. The anatomical mechanism which probably underlies a volitional muscular contraction, and a simple reflex may here be briefly described, as illustrations of neuron-chains. If we take first the example of a volitional muscular contraction we will find that a chain consisting of two neurons is involved. The cell body and dendrites of one of these is situated in the motor, cortical center of the brain, its neuraxis passes through the internal capsule, the crura and one of the pyramidal tracts of the medulla and spinal cord. Somewhere in the cord it ends in the grey matter of the anterior horn, terminating in an end-brush which is in close proximity to the cell body or the dendrites of a neuron, which forms the second link in the chain. The neur-

axis of this second neuron (the motor anterior horn cells) leaves the cord through the anterior root, enters a nerve trunk and ends in an end-brush in a voluntary muscle fiber.

In the other example chosen, the path involved in a simple reflex, the chain is also made up of two neurons. In this instance the impulse originates in the end-brush of the dendrite of a spinal ganglion neuron, is conveyed along the dendrite to the cell body of the neuron in question, thence along its neuraxis, which on entering the dorsal portion of the spinal cord divides into an ascending and descending branch, from which a number of secondary branches are given off (collateral branches); some of these secondary branches terminate in an end-brush in the anterior horn of the grey matter in adjunction with the cell body or dendrite of a motor neuron, which forms the second link in the chain. The impulses pass out along the neuraxis of this cell to a voluntary muscle fiber. The two examples chosen may serve to illustrate the more modern conception of the structure of the nervous system.

If then the entire nervous system may be looked upon as a complex of neurons, and if these are all united into nerve-chains as I have tried to show you, the most logical way of considering the sympathetic system is to treat of it as a portion of the entire nervous system, this being looked upon as a unit. This I hope to do in these lectures.

The results I wish to bring before you are in a large measure consequent upon the application of these improved methods—the Golgi and the *intra vitam* methylen-blue method—which in the hands of many investigators have in this portion of the nervous system, as well as in others, greatly extended our knowledge.

These results will be taken up under the following heads:

1. The development of the sympathetic ganglia and nerves.
2. The shape and structure of a sympathetic neuron,
  - (a) cell body and dendrite;
  - (b) neuraxis;
  - (c) the endings of the neuraxis.



3. The relation of the sympathetic neurons to—
  - (a) the cerebro-spinal system ;
  - (b) to other sympathetic neurons.
4. Sensory fibers of the sympathetic system.
5. Reflexes in the sympathetic system.

*Development of the sympathetic system.*—The entire nervous system, peripheral as well as central, has its *anlage* in a band or plate of ectodermal cells, known as the *medullary plate*, and from the ectoderm in the immediate vicinity of this plate. During the further development of embryonic *anlagen*, the edges of this plate become elevated to form the *medullary groove*, and the edges of the groove fuse to form the medullary canal, which ultimately becomes completely separated from the remaining ectoderm. The ectoderm of the medullary plate, the groove and the earlier stages of the canal, consist of a single layer of cells. At a very early stage in the development of the nervous system, indeed before the groove has been converted into a canal, a differentiation is noticed in these cells, two distinct forms being recognized. The one form, tall columnar cells, which extend from one surface of the ectoderm to the other, so-called *spongioblasts*, which develop, as has been clearly shown, into the sustentacular tissue of the central nervous system, forming the ependym and neuroglia cells: and the other form, large oval or round cells with prominent nuclei, found between the spongioblasts; these develop into nerve cells and are known as *germ cells*.

His (9) has shown that the germ cells proliferate very actively by means of karyokinetic cell division and migrate from a position near the inner wall of the medullary canal toward the outer wall. While they are thus wandering, the round or oval cell becomes pear-shaped and from the attenuated end there begins to bud a process which is the *anlage* of a neuraxis. The cells are now known as *neuroblasts*.

The processes of many of these neuroblasts grow through the ventral portion of the developing cord or brain and from the *anlagen* of motor roots.

Many of the germ cells are therefore the *anlagen* for the

motor neurons, the dendrites present in the fully developed motor neurons budding from the cell bodies at a later stage in their development. The other germ cells, that is those not developing into motor neurons, form intra-medullary neurons.

While these developmental changes are going on in the neural canal, similar changes are seen in that portion of the ectoderm just outside of the canal. In this region, even before the medullary groove has become a canal, germinal cells, like those found in the sides of the groove, wander out into the angular space between the ectoderm and closing neural canal, to form the neural crests. These neural crests, composed of germinal cells, segment, a group forming opposite each mesoblastic somite. The cells in these segments wander to a position between the neural canal and the respective somites, and form the *anlagen* for the spinal ganglia. The cells have become bipolar and are known as gangioblasts (Lenhossék), one of the processes growing into the dorsal portion of the developing neural canal, forming the posterior or sensory root, the other toward the periphery, joining the developing anterior root and forming the sensory fibers of peripheral nerves. The bipolar cells become unipolar, with "T-shaped" processes as found in the fully developed spinal ganglia, either by a fusion of a short portion of the two processes or, as Lenhossék has suggested, by drawing away of the cell body from the two processes, the extended and attenuated portion of the cell-body forming the vertical arm of the "T."

I have in this very brief account thus hastily traced the development of motor, sensory and intra-medullary neurons, and a moment's reflection will show that only the sympathetic system, and some of the special sense organs are still to be accounted for.

The development of the sympathetic system begins somewhat later than does the cerebro-spinal system.

His (10) states that, in the human embryo of 7 mm., there is as yet no evidence of the sympathetic system, while the medullary canal is completely closed, and the ganglia of all the spinal nerves as well as the anterior roots are to be seen. In a

human embryo 10 mm. in length, its *anlage* may be observed; its development falls therefore into the second month. His further states that its development begins with the development of the white rami communicantes. In a human embryo about 7 mm. in length, he describes short visceral branches, which leave the *anlagen* of the spinal nerves, a short distance beyond the junction of the anterior and posterior roots, and at a point where the spinal nerves reach the dorsal cœlom border. These branches grow in toward the aorta, and at this stage there are as yet no cells in or on these rami. In tracing the development of the sympathetic cells I shall follow the account given by His, Jr. (11). The description given has reference chiefly to observations made by him on chick embryos of the fourth day. In cross sections of such embryos passing through a spinal ganglion, small clusters of cells, the clusters numbering 2-4-10 cells respectively, are seen in the mesoblastic tissue between the point of junction of the anterior and posterior roots and the aorta. The cells in these clusters differ in structure and in their affinity to staining reagents from the surrounding mesoblastic cells.

They are of round, oval or polygonal shape, and have large nuclei and nucleoli. They stain well in hæmatoxylin and eosin, so that even under low power they may be differentiated from the surrounding mesoblastic cells. The evidence seems in favor of the supposition that these cells, which, as we will see, are the germ cells of the sympathetic ganglia, do not develop *in loco*, that is from the surrounding mesoblastic cells as was formerly believed and has quite recently been asserted by Patterson (12), but that they wander out from the spinal ganglia as germ cells possessing this motile power. The origin of these cells from the spinal ganglia was first suggested by Balfour (13) in his monograph on Elasmobranch fishes. Schenk (14) and Birdsell arrived at the same results for birds and mammals. Onody (15) has more recently, in a very comprehensive paper, in which he gives the results of his observations on the development of these structures, in the various classes of vertebrates, reached a similar conclusion.

His, Jr. (16) and Romberg were, I believe, the first to draw attention to the fact that these cells were not simply split off from the spinal ganglia, nor were they pushed out of the ganglionic *anlage* as a result of a rapid proliferation of the cells in these *anlagen*, as was held by the earlier investigators, but that they migrated from the spinal ganglia into the surrounding tissue. His, Jr. (11) describes these cells as wandering in swarms, indistinctly bounded, toward the ventral portion of the embryo. In the cervical and upper dorsal region, these migrating cells collect in larger groups on the dorsal side of the carotids, in the abdominal region, by the side of the aorta, thus forming, with the developing rami communicantes, above noted, the *anlagen* for the great sympathetic cords or chains.

At this early stage in the development of the sympathetic system the great majority of the cells are as yet apolar, and many show karyokinetic figures. From the groups of cells, forming the *anlagen* of the ganglia of the chain, germinal cells wander to a position below the aorta, to form the cœlic and the other ganglia found here. This wandering of the germ cells of sympathetic ganglia from the *anlagen* of the spinal ganglia or the larger ganglia of the chain to peripheral organs has been most clearly shown for the ganglia found in the heart. His, Jr. (11) has given us a very complete account of the way in which the germ cells reach this organ. He has studied the development of the heart nerves in fishes, amphibia and birds, also in the human embryo. It would encroach too much on the time I have set for this portion of my subject, to give a detailed account of the results obtained by him; I will therefore simply give the following conclusions reached: "That the ganglia of the heart are developed from germ cells which wander to this organ from the spinal ganglia and the sympathetic ganglia. This migration takes place by one of two paths:—in fishes and batrachians along the veins, and in birds and mammals along the arteries."

That the sympathetic ganglia which are found in connection with some of the cranial nerves are developed in the same way as are the ganglia of the great chains may be gathered from observations made by Remak (17) on chicks, of the third day of



incubation, and by Kölliker (18) on rabbit embryos 16 days old they having shown that the ciliary, the sphenopalatine and otic ganglia have their *anlage* in cells which "bud out" from the Gasserian ganglia.

In this brief sketch I have endeavored to show that the evidence is in favor of the supposition that the sympathetic ganglia of the great chains and those found on the cranial nerves, are developed from germ cells which wander out from the *anlagen* of the spinal ganglia and from the *anlagen* of the sensory ganglia on the cranial nerves. These cells are at first apolar and proliferate by karyokinetic cell division. The clusters of cells which form the beginning of the ganglionic chains are centers from whence germ cells wander to organs and tissues to form the *anlagen* of the sympathetic ganglia there found. As development proceeds, the apolar germ cells develop into sympathetic neurons by a budding out of the neuraxes and of the dendrites, this differentiation or further development being essentially the same as that described for the germ cells or neuroblasts found in the developing neural canal, which, as I have above stated, develop into the motor and intra-medullary neurons.

*Shape and structure of neurons of the sympathetic system.*—The neurons of the sympathetic system are usually found in larger or smaller groups, forming the so-called sympathetic ganglia. These ganglia vary greatly in size. Many attain dimensions great enough to make their recognition very easy, as for instance, the superior cervical ganglion, which in man is about 20 mm. long and 4 to 6 mm. broad (Quain). From ganglia of such size, every gradation in size is met with until the microscopic ganglia—the terminal ganglia—found in the various organs are reached. All sympathetic ganglia, large and small, are invested with a connective tissue capsule, which is continuous with the perineural sheath of the nerves entering and leaving the ganglion. In a general way it may be stated that the thickness of the capsule is proportionate to the size of the ganglion. From the capsule, connective tissue trabeculæ,

bands or septæ, pass into the substance of the ganglion, forming a framework.

Consequent upon results obtained by the Golgi and methylen-blue methods, we now possess very definite information concerning the shape and to some extent also the structure of the nerve cells constituting the sympathetic ganglia. Kölliker (19) as early as 1889 drew attention to the fact that the sympathetic nerve cells might be stained with the Golgi method and showed that in the mammalia these cells were multipolar. Ramon y Cajal (20) soon corroborated these results and extended them in so far as his researches also included birds, he finding that here also the sympathetic nerve cells were multipolar. Cajal further made the important discovery that, while the cells were multipolar, they possessed only one neuraxis, the other branches being dendrites.

These observations were soon confirmed by van Gehuchten (21), Retzius (22), Sala (23), v. Lenhossék (24), they also using the chrom-silver method in their several researches, and by Dogiel (25) who has studied these structures with the methylen-blue method.

My own observations confirm the results above briefly sketched, and further show that the sympathetic nerve cells of fishes and of reptilia are also multipolar. The statement that the neurons of the sympathetic system of fishes, reptilia, birds and mammalia are multipolar, needs to be qualified to this extent—that only the great majority of these cells belong to this type, a few unipolar and bipolar cells being also found. These, as Dogiel (25) has correctly stated, are usually in the peripheral portion of the ganglia, and more often near one of the poles.

My own observations on the structure of the sympathetic ganglia of vertebrates were made both with the Golgi and methylen-blue methods; the former method was however soon discarded, as in my hands the *intra vitam* methylen-blue method gave much more definite results.

These observations pertain to preparations made of sympathetic<sup>1</sup> ganglia of the following vertebrates:—

Fishes,—black and rock bass and perch, (*Micropterus dolomieu* [Raf.], *Ambloplites rupestris* [Raf.], *Perca flavescens* [Mitch.]).

Amphibia,—frog, (*Rana catesbeiana* and *Rana halecurea*).

Reptilia,—tortoise, (*Chrysemys picta*, *Chelhydra serpentina*, *Emys melegaris*).

Birds,—chicken, *Gallus domesticus*.

Mammalia,—Guinea pig, rabbit, cat and dog.

*Structure of the cell bodies of neurons of the sympathetic system.*—The structure of the cell body of nerve cells of the sympathetic system does not differ in any essential from that of motor or sensory neurons.

In sympathetic ganglia stained in methylen-blue, fixed in ammonia molybdate and sectioned, only a few of the cells in any one section are as a rule stained; some deeply, others with varying degrees of intensity, while many of the cells are entirely unstained. This enables the observer to study the development of the staining in the ganglion cells. Under high power it may readily be seen that the staining of the cell bodies is due to the fact that certain granules—*chromophile granules*—which show an especial affinity for the stain, give them their color. Chromophile granules in the cell bodies of neurons were first described by Nissl, who has further shown that in pathological conditions involving nerve cells, these granules are markedly affected. In the motor cells of the cord these granules are relatively large, giving the cell a mottled appearance. In sensory cells (spinal ganglia) they are often quite small (Lenhossék). In sympathetic nerve cells, where faintly stained, only a few very small chromophile granules are to be seen scattered more or less evenly through the protoplasm; while in more deeply stained cells the granules are more closely packed, are usually somewhat larger, and have often an angular shape. Between the

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<sup>1</sup> The results here briefly referred to will appear in a much fuller account accompanying colored plates, now in preparation.

granules an almost colorless and apparently structureless ground substance may be seen. These observations confirm very closely results obtained by Dogiel (25) with this method.

Dehler (26) has described a centrosome in the sympathetic ganglion cells of the frog. This is, as far as I am aware, the only observation of this structure in sympathetic nerve cells, although Lenhossék (27) had previously drawn attention to its existence in the spinal ganglia of the frog, and Miss Margaret Lewis (28) has quite recently found it in some large nerve cells, which she describes as giant cells, in an annelid belonging to the *Maldaniæ* family; and Schaffer (29) in the head-ganglia of *Petromyzon*.

The nuclei of sympathetic neurons are as a rule only imperfectly stained in methylen-blue. They are relatively large and often have an eccentric position, nearer the pole, opposite the one from which the neuraxis arises. Nucleoli may or may not be observed.

I wish here briefly to refer to the curious fact that in some of the rodents—rabbit, hare and Guinea pig—a large number of the sympathetic neurons possess two or even three nuclei. Attention was drawn to this fact, many years ago, by Schwalbe (30), and has quite recently been the subject of a special communication by Apolant (31). Schwalbe showed that in the ganglia of the sympathetic chain of young rabbits, mono-nuclear ganglion cells and ganglion cells with two nuclei were to be found; and that the number of the mono-nuclear cells decreased with the age of the animal. He states that in old animals the mono-nuclear ganglion cells of the sympathetic are bipolar, while those with two nuclei are multipolar.

That these are not simply degenerated cells, Apolant (31) argues may be shown by the fact the multinuclear sympathetic nerve cells are to be found in embryo rabbits of the third week. They develop, he states, by an amitotic division of the nuclei of the mono-nuclear cells. Apolant discusses the question, whether the cells with two nuclei might have two neuraxes, as suggested by Guys. His results with the methylen-blue method seem to have been unsatisfactory, and as this question



could alone be approached by a study of preparations obtained with this method, he leaves the question unanswered.

In methylen-blue preparations of sympathetic ganglia of half grown rabbits and of full grown Guinea pigs, fixed in ammonia molybdate and sectioned, I find that, in the semilunar ganglion, sympathetic cells with two nuclei are numerous, although mono-nuclear cells may easily be found. I find no fixed relation between the number of nuclei in a given cell and its shape, as has been stated by Schwalbe, i. e., bipolar cells being mono-nuclear and multi-polar cells being multi-nuclear. Multi-polar cells with one nucleus were found, as well as bipolar cells with two nuclei. In such multi-nucleated neurons in which it was possible to designate the neuraxis, only one was found. The sympathetic ganglia of rabbits and Guinea pigs, in which neurons with two nuclei were observed, are in all other respects similar in structure to the sympathetic ganglia of vertebrates having only mononuclear neurons, as will be shown later.

Apolant (31) suggests that "The development of two nuclei, in the cells in question, is in close inter relation with the growth of the cells, and in this way—the nucleus of a mono-nuclear cell attains a relatively large size (as he has shown by measurement), it then divides amitotically, this reacts on the cell body and causes it to grow proportionately. The process is therefore not a functional one, but a biological one." Apolant does however not explain why this should take place only in certain ganglia of the rabbit and not in others; in the ciliary ganglion, for instance, only mono-nuclear cells are found; and why in certain rodents and not in others, he himself having shown that in the sympathetic system of the rat, mouse and squirrel only mono-nuclear cells are to be found. This curious fact, it seems to me, still awaits explanation.

*Capsule.*—The cell body of a sympathetic neuron is surrounded by a nucleated capsule, which consists of cells resembling endothelial cells. In multi-polar cells, the dendrites pierce this capsule. Whether the capsule extends out on to the dendrites for any distance, I am unable to say positively, although the evidence points against such a view. It is generally stated

that the capsule and the neurilemma of the neuraxis are continuous; my own observations do not allow me to formulate any definite opinion on this point.

*Dendrites.*—The number and the arrangement of the dendrites of sympathetic neurons vary greatly, even in the same ganglion. As already stated, some few cells are unipolar; this is especially so in the larger ganglia. The single process present, is of course the neuraxis. In amphibia cells of this character are the general rule for all ganglia, excepting those found in the coats of the intestine.

In sympathetic cells possessing dendrites, their number may vary from one—bipolar cells—to ten or perhaps even more. These dendrites may have their origin from any portion of the cell body, as is the general rule, or several dendrites may arise from one large process, from which springs also the neuraxis. Cells of this character are prevalent in the larger ganglia of the sympathetic system of the reptilia.

The dendrites usually break up near the cell body into secondary and tertiary branches, and undergo further and repeated divisions until exceedingly fine terminal branches are reached. In well stained sections the dendrites form a very complicated network, which is found between the ganglion cells. This dendritic plexus is especially dense toward the periphery of the ganglion, as has been shown by Dogiel (25) and described by him as the "general peripheral plexus." The plexus formed by the branching dendrite is always extra-capsular, as may easily be seen in methylen-blue preparations double stained in alum carmine. In preparations well stained the cell bodies of the neurons are surrounded by a densely woven, basket-like plexus, in which the dendrites of several neurons may take part.

Ramon y Cajal (20) has described such basket-like plexuses as pericellular nests, and supposed this arrangement to be of physiological importance, believing that the sympathetic neurons were by means of it associated in their function. Dogiel (25) has, however, and I think very justly, discredited this conclusion, and, while he describes and pictures such pericellular

nests, he thinks their presence is due to an accidental arrangement of the dendrites. The fact that these pericellular nests are always extra-capsular, and that therefore the several dendritic processes which participate in their formation are not in contiguity with the cell bodies of the neurons which they surround argues very strongly against Cajal's hypothesis.

The statement has just been made that the dendrites break up into branches which terminate in the respective ganglia. Dogiel (25) has however shown that a few of the dendrites of some of the neurons in a ganglion pass beyond the bounds of said ganglion, enter a nerve trunk coming to, or leaving the ganglion and thus reach a neighboring ganglion, where, after undergoing division, they terminate. Such branches, he states, resemble very closely non-medullated nerve fibers, and only when they can be traced to the cell from which they spring, and when it can be made out that from the same cell there arises an axis-cylinder, can the true nature of these protoplasmic branches be ascertained.

*Neuraxes of sympathetic neurons.*—Sympathetic neurons are no exception to the very general rule, that a neuron has only one neuraxis. The neuraxis may spring directly from the cell body, as is commonly the case, or from one of the dendrites. In the former case the neuraxis has its beginning in a cone-shaped extension of the cell body. In the latter case it may arise from any portion of a dendrite. In some cases, as for instance in the larger cells of the sympathetic ganglia of reptilia, all processes—neuraxis and dendrites—have their origin in a single large process, which in turn arises from the depth of a depression seen on one side of the cell body. Even in such cells the neuraxis may arise from a dendrite, at a variable distance from the cell body. The fact that a neuraxis may be given off from a dendrite, is only another proof of the opinion now very prevalent, that the dendrites are only extensions of the cell protoplasm, and will therefore receive no further discussion.

In describing the structure of the neuraxes of sympathetic neurons I shall follow very closely a summary by Kölliker (32),

touching on this point. After discussing the literature and reviewing his own work, he reaches the following conclusions :

1. The neuraxes of sympathetic neurons become invested in many cases with a thin medullary sheath, thus forming very fine medullated fibers, which on account of their small size can be differentiated from the smallest cerebro-spinal fibers.

2. In some cases this thin sheath of myelin accompanies the respective neuraxis to near its termination. Such fibers, he states, are found in the ciliary branches of the ophthalmic ganglion ; in the nerves innervating the muscles of the hair papillæ (cat) ; and many of the fibers of the sympathetic chain.

3. In many of the sympathetic nerve fibers the medullary sheath is sooner or later lost, the neuraxis continuing as a non-medullated fiber ; as for instance in the intestine, the liver, and in some of the nerves going to the spleen.

4. And finally the sympathetic system contains a large number of fibers—neuraxes of sympathetic neurons—that are non-medullated throughout their whole course. The great majority of the neuraxes of the neurons in the peripheral ganglia, in the intestine, in glands and in the heart are fibers of this nature.

As regards the structure of the neuraxes of sympathetic neurons the following observations have been made—

1. Dogiel (25) has shown that they consist of very fine ultimate fibrillæ, between which there is found a very small amount of inter-fibrillar substance—the neuroplasma.

2. Dogiel (25) further states that these neuraxes have as a rule a very regular and smooth contour, and only now and then small spindle-shaped enlargements, which resemble varicose enlargements, are to be seen. My own observations would lead me to modify this statement to this extent,—that only the larger neuraxes of sympathetic neurons, such, I have reason to believe, as are invested with a sheath of myelin, show this smooth contour ; while a great many of the neuraxes (such as remain non-medullated) show the typical varicose enlargements ; it is true more often near their termination. The structure and importance of such varicose enlargements is a point concerning



which opinions differ. Without attempting to discuss this point here, I may say that I have regarded them simply as accumulations of the neuroplasma, and the fine thread uniting the globules, as the ultimate fibrillæ of the respective fiber. The observations which have suggested this hypothesis are briefly these: In fresh methylen-blue preparations in which the sympathetic nerves were well stained, examined as soon as the tissue was removed from the body, I have often noticed that the varicose enlargements, both on sympathetic fibers and ultimate branches of the cerebro-spinal nerves, are far less numerous than when the preparations are exposed to the air sometime before they are studied or when such examination is deferred until the tissues are fixed. The method of their development I have explained to myself to be the following,—when the nerve fiber begins to break down, the semi-fluid neuroplasma collects in small globules, which usually stain quite deeply; the more resistant ultimate fibrillæ unite the small globules, and give us the appearance commonly described as a varicosity of the fibers.

Very characteristic for non-medullated sympathetic fibers, that is neuraxes of sympathetic neurons not invested with myelin, is the presence of a large number of sheath-nuclei; nuclei of the sheath of Schwann.

These are much more numerous than in a medullated nerve fiber, where, as is well known, usually only one nucleus is found in an inter-nodal segment. These nuclei are often relatively large and when stained with methylen-blue, as they sometimes are, they may simulate a ganglion cell. In thin sections, however, and by double staining, their true nature may be revealed. The neuraxes of the neurons of a given sympathetic ganglion wind their way between the ganglion cells, toward the periphery of the ganglion, and enter one of the nerve trunks leaving the ganglion.

Lenhossék (24) and Dogiel (25) have observed that now and then such neuraxes give off one or several collateral branches, while yet within the ganglion, which, as Dogiel states, may branch between the ganglion cells into further branches; their mode of ending is however not known.

As already stated, sympathetic cells have only one neuraxis; the apparent exception to this rule, ganglion cells in the peripheral ganglia of the intestinal canal, as first described by Ramon y Cajal(33), has been shown to rest on faulty observation. Cajal believed that all the processes of these cells were to be looked upon as neuraxes. K  lliker(34), as he himself states, was at first inclined to accept Cajal's interpretation of these structures. Dogiel(35) has however quite recently shown that the cells in these ganglia are in structure like similar cells in other ganglia—possessing only one neuraxis, the other branches being dendrites. These observations I can fully confirm, and that on a large number of methylen-blue preparations of the intestinal wall of fishes, of amphibia, reptilia and mammalia, in which the ganglion cells of Auerbach's plexus were well stained. In every instance in which it was possible to make out clearly the shape of these ganglion cells, and trace their respective processes, only one neuraxis was made out.

The neuraxes of the sympathetic neurons thus far described carry efferent impulses. Their mode of termination may be one of the following,—

1. In involuntary muscle tissue ;
2. In heart muscle tissue ;
3. In glands ;
4. In spinal ganglia ;
5. In other sympathetic ganglia.

1. *Ending in involuntary muscle tissue.*—It is now generally believed that all non-striated muscular tissue, namely that of the intestinal canal and the gland ducts in connection with it, the smooth muscle of the urogenital system, the smooth muscle found in the skin, the eye and all vessels, receives its nerve supply from sympathetic neurons. However, only in recent years has this view received its full morphological demonstration; by which is meant, that the staining of a sympathetic neuron in its entirety has only in recent years been accomplished. The only existing figure, with which I am familiar, showing a whole neuron and its ending in involuntary muscle, is found in an article

published by Arnstein (36), on the nerve supply of the respiratory organs. Arnstein in this illustration, a portion of which is reproduced in Fig. 1, shows a sympathetic neuron, the cell body and dendrites of which are situated in a small sympathetic ganglion found in the posterior wall of the trachea, where he was able to trace the neuraxis of said neuron into the muscular tissue of the tracheal wall. Non-medulated nerve fibers—the neuraxes of sympathetic neurons—can without difficulty be stained in involuntary muscle tissue, but such fibers are usually woven into intricate plexuses, so that the tracing of a single fiber with its branches, especially when of some length, becomes a matter of extreme difficulty. I have some few times succeeded in doing this for neurons situated in Auerbach's plexus. In fishes and reptilia the sympathetic cells of this plexus are often quite isolated; this is especially true of fishes, where also the neuraxes are relatively short, so that in methylen-blue preparations the neuraxis could be traced from the cell body to its ending in the involuntary muscle cells. The neuraxes and dendrites of the neurons destined to innervate the involuntary muscle are united into an intricate plexus, at the nodes of which the cell bodies of the neurons are grouped into small ganglia. From this plexus, smaller or larger bundles of nerve fibers are given off, which form a plexus around the fasciculi of the muscle. This plexus is very well shown in the bladder of the frog, where the fasciculi form an interlacing network. From the plexus around the fasciculi, fibers or small bundles of fibers are given off, which can often be traced for longer or shorter distances between the muscle cells as they course along in the intercellular cement, and where they run parallel to the long axis of the muscle cells.

The ultimate ending of these fibers in or on the muscle cells has been a point much disputed; two very distinct views being held until quite recently, Arnold (37), Frankenhäuser (38), Lustig (39) and Obregia (40) believing that the nerve fibers terminate in the nuclei of the involuntary muscle cells, often passing through the nucleus of one cell, again entering the intermuscular plexus, and entering another cell before terminating.

Other writers, among whom may be mentioned Kölliker (41), Löwit (42), Gescheiden (43), Retzius (44), Müller (56) and Dogiel (45), state that the ultimate fibrillæ terminate on the muscle cells. To throw, if possible, some new light on this question, I have made sections,  $5\ \mu$  in thickness, of the muscular coat of the intestine of fishes, amphibia, reptilia and mammals, previously stained in methylen-blue and then double stained in alum carmine. In such preparations, when well stained in methylen-blue, only the nerve fibers show a blue color, while the muscle cells are colored in the carmine. In such sections, one may see the terminal branches of the sympathetic neurons, in the inter-cellular cement between the muscle cells; and it may be observed that all along, in their course, they give off short and exceedingly fine branches, or side twigs, which end on the muscle cells often near the nucleus, in small terminal swellings of round, oval or pear-shaped form. The terminal branches are always very varicose, and after giving off a number of "side twigs" also end on the muscle cells in the manner above described. This description corresponds very closely to those given by Erik Müller (56) and by Retzius (44), the latter having described an especially well stained, Golgi preparation made from the bladder of a rabbit 9 days old; the results obtained by the two methods being thus corroborative. In Fig. 2, may be seen the ultimate ending of the neuraxis of a sympathetic neuron on an involuntary muscle cell.

A question of some importance in this connection is the following—Do all of the muscle cells in involuntary muscle have a distinct and separate nerve supply?

Retzius (44) gives no definite answer to this question, although he inclines to the view that they do not. The answer is difficult in so far as it is impossible to determine whether all of the nerve fibers in a given preparation are stained. In preparations in which this would seem to be the case, not nearly all the muscle cells have a separate nerve ending. In the smooth muscle of the intestine the varicose, intra-fascicular branches, above referred to, have a more or less parallel course, and in my most successful preparations, three to four rows of the



spindle shaped muscle cells are usually found between two such fibers. It is of course impossible to say whether, in the preceding or succeeding sections, terminal fibers which held a very close relation to the muscle cells found between two parallel fibers, might not exist. In thicker sections, there always seem to be some muscle cells that are not touched by a nerve fiber or an ending of such fibers. I am inclined to think therefore that not all the cells in involuntary muscle have a nerve fibril ending on them.

The innervation of the involuntary muscle of vessels is best studied in relatively small vessels. In such vessels, sympathetic nerve fibers, often very varicose, form a plexus in or outside of the adventitia. Such a plexus is well shown in Fig. 3, which shows a portion of a small vessel from the pharynx of a frog, injected with methylen-blue. From this peri-vascular plexus, terminal fibers or small bundles of fibers enter the muscular media, where in thicker vessels they form an intra-muscular plexus; from the intra-muscular fibers, terminal branches arise which end on the muscle cells.

The account here given is very similar to one given by Retzius (44), who has described the innervation of the vessels in the choroid of white rabbits, also vessels of the frog's pharynx, and corroborates observations made by Dogiel (45) on the nerve supply of the vessels of the human eye-lid, to some extent also the accounts given by His and Kölliker of an earlier date.

2. *Ending of sympathetic neurons in heart muscle.*—It is not my purpose to give here the older literature bearing on this portion of my subject; for this the reader is referred to articles by Retzius (44), Berkley (46) and Jacques (47). The first communication dealing with the innervation of heart muscle, giving observations obtained either with the Golgi or methylen-blue method, we have from Arnstein (48), who describes a loose plexus around the bundles of the heart muscle cells. From it small varicose branches are given off, which may often be traced for long distances. These end on the cells without forming bulbar enlargements. In the account given by Retzius

(44) we learn that Cajal succeeded in staining the heart nerves in reptilia, batrachians and mammalia, with the rapid Golgi method (personal letter to Retzius). The nerves are described as non-medullated, forming plexuses around the heart muscle fibers, and ending in varicose fibers which terminate on the heart muscle cells in small end bulbs. Retzius' (44) description corresponds very closely to that given by Cajal and need therefore receive no further mention. Heymans (49), who cut the frog's heart stained after the Golgi method, into serial sections, reaches the conclusion, based on the richness of the nerve supply, that each heart muscle cell is directly innervated.

Berkley (46) has studied the ending of heart nerves in the white rat, the frog, sparrow and the dog, using a modified Golgi method (tissues were prefixed in picric acid). Berkley describes two kinds of fibers in the inter-muscular plexus—varicose fibers, of a brownish black color, and fibers rarely showing any knotty thickenings and giving off few branches and often showing a rounded or elongated bulb near their termination. Two kinds of endings are described:

(a) "The end-apparatus of the varicose network is usually very simple, being represented almost without exception by a minute ball-like enlargement at the terminal point of the end-branches."

(b) The second type of fiber presents an end-apparatus more complex; "an end-termination of considerable size, lying upon the sarco-s substance of a single muscular fiber may be seen." The end-apparatus of the second type is found on the fibers presenting the nodular enlargements above referred to, and Berkley looks upon these nodular enlargements as bipolar cells, situated in the path of the fiber, and suggests as a hypothesis that we may here have sensory fibers, either of the sympathetic or cerebro-spinal system.

Jacques (47) has made observations on the intrinsic heart nerves in the frog and mammals, both with the Golgi and methylen-blue method. As regards the ultimate ending of the motor nerves he has this to say in his summary:

"The nerve trunks anastomose with each other after their

entrance into the myocardium to form a fundamental myocardial plexus from which the system of intermuscular fibers originates. It is from the latter that the terminal fibers arise which penetrate between the cells of the muscle bundles and enter into communication with them by the medium of lateral and terminal branches of varied form and size, comparable for the most part to the terminations described in striped muscle of different invertebrates."

My own observations on the innervation of cardiac muscle, were made largely on the auricle of the cat's heart. The tissue was stained in methylen-blue, fixed in ammonia molybdate, sectioned and counter-stained in alum carmine. In such preparations, the plexus of non-medullated fibers around the bundles of heart muscle cells, described by other investigators, may easily be seen. In the auricular wall, numerous small ganglia, composed of sympathetic cells, are found. From such ganglia one may often trace small bundles, made up largely of non-medullated fibers (no doubt the neuraxes of the sympathetic neurons constituting the ganglia, although, owing to the fact that as a rule the cell bodies of the neurons are not stained with the methylen-blue, the tracing of the neuraxes to their respective nerve cells often becomes a matter of extreme difficulty) into the above mentioned plexus.

From such plexuses, single varicose fibers, or small bundles composed of two, three or four such fibers, can be traced between the heart muscle cells and can often be followed for some distance, giving off in their course short side branches which terminate on the heart muscle cells. The terminal endings of the side branches and the endings of the fibers differ in complexity, as may be seen from Fig. 4. In (*a*) of this figure is shown a very simple ending, the fine fiber terminating *on* the muscle cell ending in two small end bulbs. In (*b*) and (*c*) of the same figure are shown more complicated endings, the small end-branch terminating in several secondary branches which end in nodular end-swellings.

That these endings are on the heart muscle cell may be

clearly seen in double stained preparations, only the nerve fiber staining blue, the muscle cell red. This is especially well shown where a heart muscle cell and ending are cut transversely; in such a case it may be seen that the ending rests on the cell and does not in the least enter it. The more complex endings described correspond, I think, to the end-apparatus of the second type mentioned by Berkley (46). In preparations made of the auricles of a cat's heart, I find no appearances which might lead me to think that nerves having a distinctive structure are associated with characteristic endings as Berkley (46) has stated in the admirable account from which the quotations above given were taken. In the cat, nerve fibers going to the more simple and the more complex endings are distinctly varicosed, and furthermore the endings seen by me vary so in complexity, from a single small end bulb, to one with two, three, four or more nodular enlargements, that a division into two types would be a purely artificial one. In my preparations I have found no bulbous enlargements, which might be interpreted as bipolar cells, such as Berkley (46) has described. I have however often found large sheath-nuclei on the non-medullated fibers, plainly made out in double stained preparations, which, if stained with the nerve fiber after the Golgi method, might, I believe, give an appearance similar to the bulbous enlargement described by Berkley. While not denying the existence of bipolar cells in the heart, it would seem that further confirmatory observation is necessary before their presence is assured, and that with methods by means of which the structure of these nodules may be ascertained.

To summarize this portion of my subject, I may say that the neuraxis of sympathetic neurons (most probably those in the heart ganglia) terminate on the heart muscle cells either by a very simple ending, one that resembles those found in involuntary smooth muscle, or by a more complicated ending, resembling slightly the ending in striated muscle. The question may here be asked—do all heart muscle cells have a direct innervation? As already stated, Heymans (49) suggests this for the frog's heart. In well stained preparations of the auricle of a cat's heart it would appear from the number of nerve fibers



present in some fields, that this number was sufficient to innervate every cell. Sometimes two, three and in some few instances four successive cells in a given heart muscle fiber, show a nerve ending, yet when adjacent fibers were observed no endings were seen. This might of course be due to imperfect staining. Such heart muscle fibers are often touched by varicose nerve fibers, but the presence of an ending is missed. This question needs therefore further study.

3. *Ending of sympathetic nerves in gland tissues.* The problem here involved is one concerning which much has been written, yet it is only since investigators have used the Golgi and methylen-blue methods for its elucidation that anything like a definite answer could be given. As early as 1888 Retzius(50) presented to the Biological Association of Stockholm a short paper, in which the results obtained by staining the nerves of the small salivary glands, found near the papilla foliata of the rabbit, were discussed. In this account Retzius speaks of a plexus of fine varicose fibers surrounding the alveoli of the glands. He was however unable to determine what was the ultimate ending of the fibrils of this plexus or their relation to the gland cells. Ramon y Cajal(51) shortly after published results obtained by a chrome-silver impregnation of the submaxillary glands of the rat and rabbit. He here describes the non-medullated nerve fibers as entering the gland with the blood-vessels. These fibers form plexuses around the alveoli, from which fibrillæ are given off which end on the membrana propria or on the outer surface of the cells. Fusari and Panasci(52) studied the ending of nerves in the small glands of the tongue, also with the Golgi method. They state that the non-medullated fibers not only form a plexus around the alveoli but also the gland cells. Marinesco (53), who has published results obtained by staining the glands of the tongue with methylen-blue, states that both medullated and non-medullated nerves take part in the formation of the peri-alveolar plexus. From this plexus, which is external to the membrana propria, fibers pass through the membrana and end between the gland cells.

Korolkow (54), who gives in a preliminary notice results

obtained with methylen-blue staining of the salivary glands of mammalia, also finds medullated and non-medullated nerves in the glands, and was able to trace these nerve fibers through the membrana propria, and between the gland cells. In another paper Cajal (55) treats of the ending of the nerves in the pancreas. In this tissue when stained with the Golgi method, he was able to trace the ultimate branches of the nerves between the gland cells. Müller (56) corroborates in the main Cajal's results on the ending of nerves in the pancreas. He also finds that non-medullated nerves form a plexus around the alveoli—"Ein Flechtwerk von feinen Fäden, welche unmittelbar den Zellenkörpern anliegen und mit freien Endzweigen schliessen." Müller was not able to trace the ultimate fibrillæ between the gland cells. Further observations were recorded by Retzius (57) on the submaxillary glands of rabbits and dogs, in which he gives no definite account of the ultimate ending of the nerves, but mentions the existence of sympathetic ganglion cells, by the side of the ducts and blood-vessels of this gland, but states that he was not able to ascertain the distribution of the axis cylinders belonging to these cells. In another communication on the ending of nerves in the parotid of the salamander (*Salamandra maculata*) and the sublingual of lizards (*Lacerta agilis*), Retzius (58) describes inter-epithelial endings. Both of these investigations were made with the Golgi method. Dogiel (59) has studied the ending of nerves in the lachrymal glands of rabbits and Guinea pigs with the methylen-blue method. In this very admirable paper he gives the following account of the nerve endings. The nerves entering these glands are almost exclusively non-medullated. They follow the gland ducts and blood-vessels. The branches of these nerves form plexuses about the alveoli, external to the membrana propria. From these plexuses fibers are given off which pierce the membrana propria and form a second plexus between it and the gland cells, and from this second plexus, nerve fibrils pass between the gland cells, which branch, anastomose and form an intercellular network, in the meshes of which are found the gland cells. Dogiel finds no free ending on the cells; when such an

ending seemed indicated, it was interpreted as showing imperfect staining.

Berkley's (60) results on the innervation of the submaxillary gland of the rat stained with his modified Golgi method, confirm in the main results obtained by preceding investigators. On the ultimate ending of the nerves he has this to say,—two kinds of terminal endings exist: supracellular, here the ending lies on the extreme outer edge of the cell, the fibril ending in a small bulb, which rests in a pit-like depression of the surface of the cell; and inter-epithelial, of less frequent occurrence, the nerve fibril ending in the cement substance between the cells.

I wish finally to refer to a communication from Arnstein (61), "On the Morphology of the secretory nerve-apparatus." In this article Arnstein gives a summary of results obtained by himself and several of his pupils on the ultimate ending of nerves in the following glands,—mammary gland by Dmitrewsk; skin glands by Ostrowmow; prostate by Timofiew, and the pancreas, salivary glands and Harder's gland by Arnstein. Their results are summarized as follows,—the gland nerves form around the secreting tubuli or alveoli, a plexus—epilamellar plexus—which rests on the membrana propria; from this fine fibers are given off, which pierce the membrana, and as peri-cellular fibers, without forming a network, and with or without further branching, end on the gland cells in small varicose endings, the configuration and complexity of which varies for different cells, even in the same gland. These results were obtained largely on macerated and teased preparations made from glands stained in methylen-blue. In such preparations it was often possible to obtain isolated cells, showing the terminal nerve apparatus in connection with short segments of the pericellular nerves. And, if the account of Arnstein is to be trusted at all, he has given us the most complete description of the terminal ending of nerve fibers in glands. The nature of these endings may be seen in Fig. 5, taken from Arnstein's article.

I have thus reviewed the literature touching on the subject in question, partly on account of its importance, also to show



that nearly all glands have been studied either with the Golgi or the methylen-blue method and further to show that in the branched tubular or racemose glands studied a unanimity exists in the results obtained; certainly so far as pertains to grosser distribution of the nerve fibers. It may be seen that bundles of nerve fibers, largely composed of non-medullated fibers, or in other words of the neuraxes of sympathetic neurons, enter the gland with the gland ducts and with the vessels. On entering the glands they form a plexus around the branches of the ducts and vessels, from which fibers or small bundles of fibers are given off which surround the secreting alveoli or tubuli to form the epilamellar plexus. Concerning the mode of the terminal ending, opinions differ as yet. The greater portion of the evidence points however to an ending on the gland cells, either in a free ending or in a small end-bulb or, as the work of Arnstein and his pupils would show, in a more complicated end-apparatus, resting on the cells. That the non-medullated nerve fibers found in the glands are the neuraxes of sympathetic neurons, may be seen in sublingual or submaxillary glands; where, especially in the latter, large numbers of small ganglia are found in the gland itself. The writer (62), in an article in which he discusses the innervation of the sublingual and the submaxillary glands in the dog, has shown that these ganglia, which are situated in the connective tissue surrounding the gland ducts, are composed of sympathetic nerve cells. In tissue impregnated after the Golgi method and cut so that the plane of section is more or less parallel with the gland ducts, the neuraxes of the sympathetic neurons may often be followed for long distances by the side of the gland ducts, their branches forming the plexus surrounding the ducts above referred to. In a few instances a neuraxis coming from a sympathetic nerve cell, which was observed following a duct, could be followed as it left a duct and approached a group of alveoli; and in one instance of a section of a chorda-lingual triangle, which contained a portion of a sublingual gland, two sympathetic cells deeply stained were seen, the axis cylinder of one of which could be followed for quite a distance by the side of an inter-



lobular duct, and after a very short interruption a fiber of the same size and appearance, and which seemed to be a direct continuation of the axis cylinder just mentioned, could be traced into a peri-alveolar—epilamellar—plexus.

The medullated fibers which enter the glands, do not, I am inclined to think, enter into the formation of the epilamellar plexuses, as Fusari and Panasci, and Korolkow have suggested. Medullated nerve fibers, of cerebro-spinal origin are undoubtedly found in glands, and have I believe two distinct modes of termination. Some of these fibers are no doubt sensory, ending in free endings between the columnar cells lining the gland ducts. The free endings described by Arnstein (61) and myself, (62) belong I believe to fibers of this nature. Other medullated fibers end in baskets around the sympathetic cells, as pointed out by the writer. These fibers will be given no further consideration now, but will receive due consideration in one of the following lectures. From what has been said, and especially if we extend our consideration to glands which in their fully developed condition are not classed as tubular or alveolar glands; (we may refer here to work done by Berkley (63) on the intrinsic nerves of the liver, who states that such nerves are non-medullated; and the thyroid, where Anderson (64) and Berkley (65) have shown that non-medullated nerve fibers enter this gland with the blood-vessels, there to form peri-follicular meshworks, the terminal branches of which end on the gland cells (Berkley); and the supra-renal, worked on quite recently by Dogiel (66) where he has shown that the intrinsic nerves are non-medullated, in part neuraxes of sympathetic nerve cells found in this gland) we may see that the general statement, that gland cells are innervated by the terminal branches of the neuraxes of sympathetic neurons, is based on abundant observation, even though we must say [with Arnstein (61), "That many an eye will tire before the secretory nerve-endings will in their true nature be fully understood."

4. *The ending of the neuraxes of sympathetic neurons in the spinal ganglia.*—The existence of sympathetic nerves in the spinal ganglia is a point concerning which there exists as yet

some doubt. The facts we possess, pointing to such fibers are the following. In Ehrlich's (4) first publication, on the reaction of methylen-blue on living nerve tissues, he describes a very delicate network enclosing the cell bodies of some of the spinal ganglion cells of the frog. The nature of this network could however not be ascertained. Aronson (67), in a dissertation which followed Ehrlich's paper, briefly mentions similar pericellular networks, or baskets, found in the spinal ganglia of the rabbit. Such pericellular baskets were then described by Ramon y Cajal (68), seen (presumably) in the spinal ganglia of the rat, as the figure he gives in his summary of the histological structure of the central nervous system was made from a Golgi preparation of a young rat. Cajal here suggests that these baskets may represent the endings of sympathetic nerve fibers, which he was able to trace through the rami communicantes into sympathetic ganglia. These sympathetic fibers, divided in the spinal ganglia into two or three branches, which could be traced into the substance of the ganglion, where he suggests they may end in the pericellular baskets.

Dogiel (69) in a recent publication on the structure of the spinal ganglia of mammalia (dogs, cats, rabbits and Guinea pigs having been investigated) gives the following description of these structures.

"It may now and then be seen, that through an anterior branch of one of the spinal nerves a few small, medullated, sympathetic fibers enter a spinal ganglion. These at a node of Ranvier give off one or two small medullated or non-medullated branches."

These branches, medullated and non-medullated, the medullated fibers soon losing their myelin, approach a spinal ganglion cell, and, after making a few twists about its nerve-process, break up into an extra-capsular plexus, from which fibers proceed, which pierce the capsule to form a pericellular basket. Dogiel is inclined to believe that the cell bodies around which these sympathetic fibers form pericellular baskets belong to peculiar neurons found in the spinal ganglia, and first described by him. To these he has given the name, "*spinal*

*ganglion cells of the second type.*" The type two cells have the following peculiarity.—The neuraxis of such a cell, breaks up within the ganglion into a large number of branches, which, like the neuraxis, are myelated. These branches soon lose their myelin and terminate in peri-cellular baskets, enclosing the cell bodies of the spinal neurons of *type one*, the cells commonly known as spinal ganglion cells. So that, as may be seen, although relatively few sympathetic fibers enter a spinal ganglion, yet through the cells of type two, they may exert an influence over a large number of the typical spinal ganglion cells.

I may add that Dogiel looks on the sympathetic nerve fibers ending in the spinal ganglia as the neuraxes of *sensory sympathetic cells*, a type of sympathetic cells which he has described. These will be further discussed in the next section.

Finally, I may briefly mention some observations made by the writer (70) and recorded in a short paper on the spinal ganglia of amphibia.

In a number of methylen-blue preparations of the spinal ganglia of the large bull-frog, I have observed fine nerve fibers, which are sometimes wound spirally about an axis-cylinder or have a very tortuous course and break up into a network of finer branches, which terminate within the capsule of ganglion cells, from the axis-cylinders of which short processes, which end in disc-like expansions, are given off. I suggest, as an hypothesis, that this network represents the ending of sympathetic fibers found in the spinal ganglia of frogs. In some few instances I was able to trace such non-medullated fibers some distance from the cells on which they end, toward a bundle of sympathetic nerve fibers, which seemed to come from the distal portion of the spinal ganglion. Peri-cellular baskets have further been found in the vagus ganglia of the frog, also in the spinal ganglia of *chrysemys picta*, a small tortoise examined by me. Such baskets could not however be connected with nerve fibers.

5. *Ending of the neuraxes of sympathetic neurons in other sympathetic ganglia.*—Before discussing this mode of termina-

tion of neuraxes of sympathetic neurons, I wish to refer to some observations recently published by Dogiel (71), wherein he states that in sympathetic ganglia two types of sympathetic nerve cells are found. The cells belonging to the first type have been the subject of discussion thus far, and are, according to the ending of their neuraxes, either motor, ending in involuntary or heart muscle; vaso-motor ending in blood-vessels; and what we may term secretory nerve fibers, ending on gland cells. The dendrites of such neurons usually end within the respective ganglion in a manner previously described.

The cells of the second type are described by Dogiel as follows:—The cell body of such cells is as a rule somewhat larger than that of the cells of the first type (motor cell etc.). The number of their dendrites varies from five to sixteen or even more. These dendrites are much longer than the dendrites of the cells of the first type, undergo less branching and may often be traced as fine varicose branches beyond the bounds of the ganglion. In preparations of the ganglion cells of Auerbach's plexus, the dendrites of the cells of the second type were now and then traced into the submucosa of the intestine, and in such instances they resemble very closely axis-cylinders. Dogiel thinks that the cells of this structure are sensory sympathetic cells and suggests the possibility of their forming sensory endings in the epithelium. The neuraxes of these cells may arise either from the cell body directly or from one of the protoplasmic branches. They leave the ganglion through one of its nerve roots, in which they may become invested with a thin layer of myelin. They could now and then be traced into another ganglion, where one, two or three branches were given off. These branches, which may or may not be myelinated, break up into secondary branches, which take part in the formation of the inter-cellular plexus of the ganglion. The axis-cylinder may pass on and terminate in another ganglion. Dogiel states it quite probable that the sympathetic fibers which end in pericellular baskets about the cell bodies of the spinal ganglion cells



of type two as above mentioned, are the neuraxes of sensory sympathetic cells.

The relation of the sensory sympathetic cells to other structures is well shown in Fig. 6 copied from Dogiel's paper. The importance of these observations, in case they receive corroboration, can not be over-estimated. The existence of sensory sympathetic cells would explain certain phenomena which have been observed in connection with the sympathetic system. I may mention, for instance, peripheral reflexes and peristaltic movements of the intestine, etc. These points will however receive fuller discussion at another time.

It is not my purpose to discuss fully at this time, the question of the ending of the neuraxes of sympathetic neurons in sympathetic ganglia. In order to do that it would be necessary for me to mention certain important structures found in sympathetic ganglia, to which I have not as yet alluded, and which are more fittingly discussed in the next division of my subject; and also to refer to some very important physiological work, in connection with the sympathetic system, which has been done by Langley and some of his pupils, the discussion of which I desire to defer until the above mentioned structures have received due attention. Mention may however be made of the fact that Lenhossék (24) has observed, in Golgi preparations made of embryo chicks of the 14th day, sympathetic fibers that enter a sympathetic ganglion from the periphery, there to terminate in free endings, endings which he describes as "simple end-brushes," the fibrillæ of such end-brushes often terminating on cells in small end-bulbs.

In methylen-blue preparations of the ganglia of the chain taken from mammalia and birds, I have often observed a free ending of branches of non-medullated nerve fibers in sympathetic ganglia; not however on the cell bodies of the sympathetic neurons as Lenhossék would have us believe, but on the dendrites of sympathetic neurons. Fig. 7 shows such an ending, sketched from a moderately thin section of a sympathetic ganglion of a cat, stained in methylen-blue. As may be seen from

the figure, the end-branch of the non-medulated fiber terminates in several very small nodular enlargements.

The fiber thus ending did not seem to enter the ganglion from the periphery, or, to state it in an other form, did not seem to be the termination of a neuraxis, a part of a sympathetic neuron, situated distal to the ganglion in which said ending was found. I am free to admit, that in sections such orientation becomes a matter of extreme difficulty. Yet, in larger ganglia, studied as a whole, even when cleared in glycerine, and especially if the ganglion is at all well stained, the tracing of nerve fibers and the recognizing of their mode of ending is to me a task more beset with difficulties and more open to misinterpretation. Hence the reason for studying the larger ganglia in sections. I may say that the observation here presented is not unique, but has been met with many times. Whether the free ending on the dendrites of sympathetic cells, is to be looked upon as the ending of neuraxes of sensory sympathetic neurons, in the sense suggested by Dogiel, I am unable to say. I would suggest, however, as an hypothesis, the possibility of a similar ending for the neuraxes of sympathetic neurons, situated central to the ganglion in which they end, neurons not sensory in their nature. This point will, however, as above stated, be taken up again.

*Ending of cerebro-spinal nerve fibers in the sympathetic ganglia.*

—In methylen-blue stained sympathetic ganglia there are always found a varying number of medullated nerve fibers. Some of these medullated fibers pass through the sympathetic ganglia, without in any way making connection with the sympathetic nerve cells contained therein; these are in all probability sensory, cerebro-spinal fibers, and will be discussed at a future time. Other medullated fibers terminate in the sympathetic ganglia, by ending in peri-cellular baskets, which surround the cell bodies of the sympathetic neurons. These fibers will now be more fully considered.

Ehrlich (4) in his first communication on the reaction of methylen-blue on living nerve tissues, described a plexus of fine fibrillæ about the cell bodies of the sympathetic nerve cells

of the frog, which was in connection with the spiral process of these cells. Ehrlich's observations were soon confirmed by Retzius (72), Smirnow (73) and Arnstein. About the same time Aronson (67) described and pictured peri-cellular plexuses in methylen-blue stained ganglia of the rabbit—superior cervical, coeliac and cardiac. They were then described by Sala (23), Van Gehuchten (21) and Lenhossék (24) in Golgi preparations of the sympathetic ganglia of mammalia, and in more recent years by Dogiel (25) and Kölliker (34) and a number of other investigators. The peri-cellular plexuses or baskets have thus been found in the various ganglia of the chain, in the prevertebral and terminal ganglia.

They are, as will be shown, always intra-capsular, in direct contact with the cell bodies of the sympathetic neurons, within the capsule of which they are found; and are therefore not to be confused with the *peri-cellular nests* described by Cajal, which, as will be remembered, are extra-capsular.

In giving a fuller description of these structures as found in the various vertebrates, I shall take up first the mammalia, then birds, reptiles, amphibia and fishes in the order named.

(a) *Mammalia*. The peri-cellular baskets, about the sympathetic cells of mammalia, vary greatly in complexity, even in the same ganglion. A typical one may be described as follows, a section of a sympathetic ganglion of a cat or dog, stained in methylen-blue and counter-stained in alum carmine serving for purpose of description. In such preparations the cell bodies of the sympathetic neurons are stained a pale red, the axis-cylinders and baskets are alone stained blue. In such preparations it may be seen that one, two, three or even more, small varicose nerve fibers approach a ganglion cell and before or after piercing the capsule, they break up into a number of smaller branches, which in turn may or may not undergo further division and then anastomose or interlace to form a plexus around the cell body of the ganglion cell in question. It seems to me that the complexity and the arrangement of the fibrillæ in the network constituting the so-called peri-cellular baskets are largely accidental and not to be looked upon as showing

essential structural differences. The fibrillæ of the peri-cellular baskets are as a rule very varicose, and often present quite large nodular enlargements. In *a*, of Fig. 8, a cell body of a sympathetic ganglion cell with peri-cellular baskets, from a sympathetic ganglion of a dog, is reproduced.

It would seem that now and then a large number of fibers take part in the formation of such baskets. Sala (23) describes small bundles of nerve fibers, which in their course give off one or several fine branches, which take part in the formation of such baskets. This condition has not been met with by me. Aronson (67) states that the nerve fibers are often wound spirally about the neuraxis of the ganglion cell, before breaking up into the baskets. I have seen this only a very few times in mammalia, and believe it not to be as common as Aronson's account would lead one to infer. In all mammalia studied these peri-cellular baskets have essentially the same structure and, as already stated, have been found in nearly all sympathetic ganglia. In the ganglia of the chain they have been repeatedly described. They were seen by Kölliker and Michel (74) in the ciliary ganglion of the cat; by Lenhossék (24) in the sphenopalatine ganglion of the mouse; by me (62) in the sublingual and the submaxillary ganglion of the dog; by Aronson (67) in the cardiac ganglia of the rabbit; by Arnstein (36) in the sympathetic ganglia of the trachea and bronchi; by Dogiel (35) in the ganglia of the intestinal canal; by Timofiew (75) in the sympathetic ganglia of the epididymis. They have further been seen by me in the sympathetic ganglia of the bladder and prostate of the cat, and in those of the œsophagus of the cat and rabbit. It would therefore seem safe to assume, that these structures are found in all the sympathetic ganglia of the mammalia.

That these peri-cellular baskets are the mode of ending of many of the medullated fibers in the sympathetic ganglia there can be no doubt, the medullated fibers losing their sheath of myelin at a variable distance from the baskets, the neuraxes continuing as varicose non-medullated fibers. Van Gehuchten (21), Dogiel (25) and Kölliker (34) have shown that many of



the medullated fibers in the sympathetic ganglia divide into branches, from which collateral branches (as a rule non-medullated) are given off, so that, as Dogiel (25) has pointed out, a single medullated fiber may end, according to the number of collateral branches present, in a number of peri-cellular baskets.

(b). *Birds*. In birds (chicken) the peri-cellular baskets in the sympathetic ganglia have essentially the same structure as those found in mammalia, and are also the endings of medullated fibers in the ganglia. The fibrillæ of the network forming the peri-cellular baskets in birds are on an average somewhat finer and not so numerous as in mammalia, so that as a whole the baskets are somewhat simpler. They are always intra-capsular. In Fig. 8, *b*, are shown two ganglion cells from one of the dorsal sympathetic ganglia of a chicken, where a small varicose fiber breaks up into two branches, each of which ends in a peri-cellular basket.

(c) *Reptilia*. In the tortoise the structures in question vary greatly in complexity. Many of the peri-cellular baskets resemble in structure those found in sympathetic ganglia of mammalia and birds; this is more especially the case in the smaller ganglia—the cardiac ganglia and the smaller ganglia of the chain. The cells enclosed in such baskets are usually multipolar, resembling in shape those found in mammalia and birds. But, as previously stated, many of the sympathetic neurons of reptilia (and this is more especially true of the larger ganglia) are relatively large and of peculiar form. The cell body of such neurons may be round or oval, and from it springs one large process, which may be straight or twisted around the cell body or upon itself. In either case, it breaks up at a variable distance from the cell body into several large branches one of which becomes a neuraxis, the others being dendrites. The peri-cellular baskets found enclosing such cells are usually much more complicated than those found about the multipolar cells, above described. The medullated fiber ending in these more complex baskets is often wound spirally around the neuraxis of the sympathetic cell, and about the large process from which the neuraxis springs, before breaking up into the fibrillæ form-

ing the network of the baskets. The number of the turns of such a spiral may vary from two to fifteen or even twenty. Several medullated fibers may take part in the formation of such a spiral. The neuraxes of the nerve fibers of such spirals break up into nerve fibrillæ, which may also be given off from some loop of the spiral, and these are woven into a complex network to form the basket. The fibrillæ of the complex baskets are usually very varicose. The spirals and end-baskets are intra-capsular. Such baskets have often been found in the inferior cervical and the stellate ganglia. In the smaller ganglia of the chain—dorsal, lumbar and caudal—there is, as a rule, found only here and there one of the more complex baskets. In C, of Fig. 8, are shown two sympathetic cells, from a sympathetic ganglion of a reptile, the one surrounded by a pericellular basket of the simpler type, the other more complex with a spiral fiber.

(d) *Amphibia*. The cells of the sympathetic system of the frog have, since they were first described by Arnold and Beale, been the subject of numerous contributions. These cells were described among the older writers as bipolar, with straight and spiral processes. Ehrlich, as has been shown, discovered that the spiral process terminated in a peri-cellular network. Ehrlich (4) regarded the spiral fiber as of cerebro-spinal origin, largely because it was invested with a layer of myelin. Retzius (72) corroborated Ehrlich's observations and further showed that the spiral fiber often branched "T"-shaped, at a variable distance from the cell on which it ends in a basket. Retzius also believes the spiral of cerebro-spinal origin. In a communication published by Arnstein (73) giving the results of an investigation by himself and Smirnow, of the sympathetic ganglia of the frog, when stained with methylen-blue, and in a further publication by Smirnow (76), very different conclusions are reached. They describe the spiral fiber as going to the periphery, and according to Smirnow ending according to the location of the ganglion in various peripheral tissues.

Smirnow further states that the spiral serves form anastomosis between ganglion cells, the spiral dividing, one branch

going to the periphery, the other going to another ganglion cell.

In *d* of Fig. 8 is shown a ganglion cell of the sympathetic of a frog. This was sketched from a section of a sympathetic ganglion, stained in methylen-blue and counter-stained in alum carmine. As may be seen in the figure, the peri-cellular plexus (basket) is intra-capsular, as described by Retzius, and encloses the cell body, as stated by Ehrlich (4), Retzius (72), Arnstein (73), and Smirnow (76); and does not, as for instance Feist (77) suggests, form a portion of the cell body. Double stained preparations leave no doubt concerning this question. The figure further shows that this basket is formed by branches of the spiral fiber, as first accurately described by Ehrlich (4). We have I believe, very strong evidence, that these spiral fibers do not go to the periphery, but are the terminal branches of medullated fibers ending in baskets. In ganglia partially stained in methylen-blue, fixed in picrate of ammonia and cleared in glycerine, medullated nerve fibers can often be traced for long distances, and their mode of ending clearly made out. In Fig. 9 is reproduced a sketch of such a fiber drawn under the 1-12 oil immersion with the aid of a camera lucida and then reduced to two-fifteenths. At the top of the figure is seen a medullated nerve fiber, a fiber which entered a ganglion through a white ramus. The course and branchings of the fiber are shown in the figure. As may be seen, a number of the non-medullated branches were traced into end baskets.

The "T" division described by Retzius (72), and the anastomosis between ganglion cells suggested by Smirnow (76) may I believe be explained on the supposition of incomplete staining of a medullated fiber the branches of which end in end-baskets.

I should thus regard the sympathetic neurons of the frog as unipolar cells, the straight process being the neuraxis of such cells, the spiral fibers the ending of another neuron, as Kölliker (34) has previously stated.

(e.) *Fishes.* In fishes the peri-cellular baskets are as a rule somewhat simpler than in other vertebrates, simpler in so

far that the terminal fibrillæ of the nerve fibers ending in these structures are not always woven into a network.

In *E*, of Fig. 8, is shown a nerve cell from a sympathetic ganglion of a black bass. It may be seen that the nerve fibers ending on the cell, (intra-capsular ending), break up into a number of varicose fibrillæ which only partly surround the cell. The endings are often more complex, but the cell shown in the figure may serve as an illustration. In fishes, as in other vertebrates, the end basket, or the intra-capsular end-brush, as it may be more correctly termed, represents the termination of a medullated nerve fiber found in the sympathetic ganglia.

From this review of the structure of the peri-cellular end-baskets in the sympathetic ganglia of vertebrates, we may deduce the following facts:

1. These structures are found in the various classes of vertebrates.

2. In all vertebrates they are intra-capsular, and have essentially the same structure. The fact that in some vertebrates—amphibia and reptilia—the nerve fiber terminating in the end-basket is wound spirally about the neuraxis of the ganglion cell, does not modify this statement.

3. In all vertebrates these peri-cellular baskets are the mode of ending of medullated nerve fibers found in the sympathetic ganglion, medullated fibers which often divide and give off collateral branches, which in their turn end in the baskets.

These questions may now be asked. Where do these medullated fibers come from; are they neuraxes or dendrites of neurons; are the cell bodies of such neurons found within or outside of the ganglion; and if outside of the ganglion, in some portion of the cerebro-spinal axis?

In answering these questions, I may at the outstart state that all the evidence we possess—experimental and histological—goes to show that these medullated fibers enter the sympathetic ganglia through the white rami communicantes. This evidence is in brief as follows:

In the first place let me draw your attention to the fact that “all effects which can be produced by stimulating the sym-



pathetic in any region, can be produced by stimulating the spinal nerves in the vertebral canal, or by stimulating the cord itself." I infer from Langley's (78) account (from whom this statement was taken) that Budge and Waller were the first to discover this fact; it has however since been repeatedly shown by other investigators.

Attention has already been drawn to the fact that the sympathetic ganglia of the chain and the pre-vertebral ganglia are connected with the spinal nerves by nerves known as the white and grey rami communicantes. The efferent impulse excited, on stimulating the cord or a spinal nerve within the vertebral canal, must therefore reach the sympathetic, through one of these communicating branches. On making sections of the white and grey rami it may be seen that the white rami consist almost entirely of medullated fibers, while the grey rami contain a great many non-medullated fibers. Gaskell (79) has shown that the majority of the medullated nerves of the white rami are unusually small, varying in size from  $1.8 \mu$  to  $2.7 \mu$ . He has further shown that in some of the anterior spinal roots nerves of the same size and structure are to be found. To state this in another form and to quote again from Gaskell, sections of the several anterior spinal roots reveal these facts:—In sections of the anterior roots of the cervical nerves, hardened in osmic acid, the great majority of the nerve fibers are large medullated fibers, varying in size from  $14.4 \mu$  to  $19 \mu$ , a few smaller fibers, not less than  $3.6 \mu$  in diameter, are also found. The first thoracic anterior root has essentially the same structure. Beginning with the second thoracic nerve, all the anterior roots to the third lumbar contain the small medullated fibers above referred to, fibers of  $1.8 \mu$  to  $2.7 \mu$  in thickness, and these can be traced into the white rami. It follows, then, that only these spinal nerves have white rami. Langley (78) who has examined the dog, cat and rabbit with reference to this point, states that the uppermost white ramus is given off from the first thoracic nerve, the lowermost probably from the fourth lumbar.

All the spinal nerves have grey rami, which, as above stated, consist largely of non-medullated fibers. Since no non-medullated nerves leave the cerebro-spinal axis through either its anterior or posterior root (Gaskell, 79) and since "the first thoracic spinal nerve, the uppermost nerve which has a white ramus, is the uppermost nerve which on stimulation produces sympathetic effect" (Langley, 78) and since, further, the white rami can be traced into the sympathetic ganglia of the chain and the pre-vertebral ganglia, it follows that a stimulus applied to a spinal nerve in the vertebral canal or to the cord itself, producing a sympathetic effect, excites an impulse which travels along nerve fibers contained in the anterior roots and thence passes through the white rami to the sympathetic ganglia.

Gaskell (79) expresses this thought in the following language:—

"The white rami communicantes are formed by an out-flow of medullated fibers from both anterior and posterior roots of the spinal nerves between the second thoracic and second lumbar inclusive (the fibers from the posterior root are probably sensory as will be explained later), which medullated nerves pass not only into their metameric sympathetic (lateral) ganglia, but also form three main streams, upwards into the cervical ganglia, downwards into the lumbar and sacral ganglia, and outwards into the collateral (pre-vertebral) ganglia."

"The white rami communicantes alone constitute the rami viscerales of the morphologist. The out flow of visceral nerves from the central nervous system into the so-called sympathetic system takes place by their means alone."

To bring these points more closely before you, I may describe briefly some of the physiological effects observed in stimulating the cervical sympathetic. It is well known that by stimulating the cervical sympathetic of the dog, cat or rabbit the pupil becomes dilated, there is an increase in the secretion from the sub-maxillary gland and a constriction of the small vessels of the ear, conjunctiva and other parts of the head. These same changes may be observed on stimulating the superior cervical ganglion directly, or on stimulating some of the nerves given

off from this ganglion. It has further been shown (Langley and others), that the same physiological effects may be produced on stimulating the upper thoracic nerves in the vertebral canal. To be more explicit and to follow Langley's (78) account, we find that "the pupil receives dilator fibers from the Ist, IInd, IIIrd thoracic nerves. The relative effect of these nerves varies somewhat in different animals of the same species, and varies considerably in animals of different species." "In the dog and cat the Ist, IInd, IIIrd, IVth and sometimes also the Vth thoracic nerves, contain vaso-motor fibers for the head, while in the rabbit the IInd to the VIIth thoracic nerves carry such fibers." In the dog and cat Langley found that "the second thoracic nerve carried the greatest number of the fibers which on stimulation cause a secretion of the submaxillary gland; although the IIIrd, IVth and Vth (the latter in the cat) carried such fibers." From these results we learn that an impulse, which leaves the spinal cord through the upper thoracic nerves, is carried along nerve fibers in the cervical sympathetic to the superior cervical ganglion, and from there to the head (vaso-motor); to the eye (pupil dilators); and to the submaxillary gland (secretory).

This question may now be asked. What relation do the small medullated fibers which leave the spinal cord through the anterior roots and pass through the white rami to the sympathetic ganglia and which, as has been shown, on stimulation cause physiological effects similar to those obtained when the ganglia or their nervous branches are directly stimulated hold to the sympathetic nerve cells of the ganglia? Do they pass through the ganglia, or do they end therein?

The physiologists have aided very materially in the solution of this problem, and of their number, especial credit must be given to Professor Langley, who through his untiring search and wonderfully exact work has done so much to give us a better understanding of the physiology of the sympathetic system.

The work to which I wish especially to refer at this point is the following :

Langley and Dickinson (80-81) have shown that "after

the injection of a certain dose of nicotin, stimulation of the cervical sympathetic, below the superior cervical ganglion, does not produce dilation of the pupil or constriction of the vessels of the ear, while stimulation of the sympathetic nerve fibers above the ganglion produces these changes in the normal manner." This, as they suggest, might be due to the fact that the medullated fibers below the ganglion are paralyzed and not the non-medullated fibers above the ganglion. That the medullated fibers as such are not paralyzed is shown by the fact that, at a time when stimulation of the cervical sympathetic does not cause dilation of the pupil, stimulation of the sciatic causes a normal contraction of the muscles supplied by this nerve. They have, however, offered a much better proof in the following experiment:

The cervical sympathetic was exposed and painted with a 1 % solution of nicotin. The nerve was then stimulated at intervals of about two minutes, central to the area over which nicotin had been painted. Such stimulation always produced a normal effect. However, on painting, the superior cervical ganglion with a similar solution, stimulation of the cervical sympathetic had no effect, while stimulation of the nerve filaments above the ganglion produced a normal effect. They conclude therefore that "Nicotin paralyzes the cells of the superior cervical ganglion," and further that "the dilator fibers for the pupil, the vaso-constrictor fibers for the ear (probably also those for the head generally) and the secretory fibers for the glands end in cells of the superior cervical ganglion."

As a result of these and other observations with nicotin the following conclusion is reached by them,—“That by stimulating a nerve fiber running to and those running from any peripheral ganglion, before and after the application of nicotin to it, the class of nerve fibers which end in the nerve cells of the ganglion can be distinguished from those which run through the ganglion without being connected with the nerve cells.”

Langley, Anderson and Dickinson and Sherrington have shown, in a series of important contributions, which have ap-



peared since the publication of the article from which the above quotations were taken, that these conclusions, as first enunciated, are correct.

We see therefore that an impulse, set up in a nerve fiber coming from the spinal cord through the anterior root and through a white ramus to a sympathetic ganglion, passes through a nerve cell before reaching its destination. Langley (82) has suggested the term pre-ganglionic (pre-cellular) fiber, to designate the efferent medullated sympathetic fibers before they have traversed the nerve cell, and post-ganglionic (post-cellular) fiber, for the sympathetic fibers after they have traversed the nerve cell. He states "that these terms involve the view that each sympathetic nerve fiber has a nerve cell on its course in one ganglion and in one ganglion only." And further,—“In saying that a nerve fiber ‘traverses a nerve cell’ or ‘has a nerve cell on its course,’ or ‘becomes connected with a nerve cell,’ I mean that a nervous impulse set up in a fiber on issuing from the spinal cord passes through a nerve cell before it reaches the periphery; I express no opinion as to the histological connection of the nerve cell with the incoming or with the outgoing nerve fiber. And I express no opinion as to whether there is any branching of pre-ganglionic nerve fibers, but that if such branching occurs, then each branch must have a nerve cell on its course.”

It seems to me that we have every fact in favor of the supposition that the pre-ganglionic fibers of Langley, which enter the ganglia through the rami, are the medullated fibers which in Golgi and methylen-blue preparations can be traced into the ganglia, and which as previously stated end in intra-capsular, peri-cellular baskets, these baskets forming the histological connection between the pre-ganglionic fibers and the nerve cells of the ganglia. That the pre-ganglionic fibers branch, a possibility mentioned by Langley (82), has been shown by a number of investigators, and may be seen in Fig. 9. The branches probably all have end-baskets, although it is a difficult task to demonstrate that fact. Fig. 9 shows that many certainly do.

The pre-ganglionic nerve fibers with their terminal baskets are the neuraxes and end-brushes of cerebro-spinal neurons which leave the cord through the anterior root. The exact location of the cell bodies of these neurons is not as yet known. Gaskell (78) has attempted to place them in Clarke's columns of the cord. It is now, however, well known that the neurons, the cell bodies of which constitute Clarke's columns, are intra-medullary neurons, the neuraxes of which form the direct cerebellar tracts.

I question the advisability of speaking of the pre-ganglionic fibers as sympathetic fibers, as Langley does in his articles. It is true they end in the sympathetic ganglia. Yet the cell bodies of these neurons are undoubtedly in the cerebro-spinal axis. They develop very much as do the motor neurons, and are, as His (10) has shown, to be seen in the human embryo before the *anlagen* for the sympathetic ganglion can be made out. They are cerebro-spinal fibers, forming a portion of a link in a neuron chain, the terminal link of which is formed by a sympathetic neuron. Neither can I consider the term "visceral nerves" used by Gaskell and others as consistent, as all of these nerves do not end in the viscera.

Some term expressing their central or cerebro-spinal origin, would seem to me more appropriate, and for want of a better term they may be spoken of as *central fibers*.

The post-ganglionic, or post-cellular fibers of Langley (82) are the neuraxes of the sympathetic neurons of the ganglion, a part of the sympathetic cell, and therefore not post-cellular. These fibers are the sympathetic nerves, neuraxes of sympathetic neurons, which as has previously been shown, end in involuntary muscle, in heart muscle and in the glands.

In Langley's writings, the statement that nicotin paralyzes the ganglion cells of the sympathetic ganglia repeatedly occurs. His reason for such a statement is, of course, based on the fact that the effects which are produced when stimulating the central (pre-ganglionic) fibers of a ganglion, can not be obtained when the ganglion, in which said central fibers end, is painted with a dilute solution of nicotin, but are obtained when the

neuraxes of the sympathetic neurons of the ganglion (post-ganglionic fibers) are stimulated directly. In discussing this point with Prof. Cushney, and taking into consideration, what is now well known concerning the minute anatomy of the sympathetic ganglia, with especial reference to the histological connection between the central, the cerebro-spinal fibers, and the sympathetic cells, we have reached the conclusion that nicotin does not paralyze primarily the sympathetic cells, but rather the intra-capsular, peri-cellular baskets of the central fibers. This conclusion is based largely on the analogy which exists between the physiological action of certain drugs—curare, spartan and others—and nicotin.

For example, it is well known that curare paralyzes the motor endings in striated muscle. That the endings, and not the muscle or the cell body of the neuron terminating in said muscle is paralyzed can easily be shown by well known physiological experiments, which it will not be necessary to mention at this place. Langley and Anderson (83) have shown that curare in large doses paralyzes also "the *cells* of the ciliary ganglion." That is, when large doses of curare are injected, stimulation of the IIIrd cranial nerve does not cause constriction or closure of the pupil.

Langley and Anderson (83) have also shown "that ten milligrams of nicotin is sufficient to paralyze the nerve-ending of the extrinsic muscles (striated muscles) of the eye. But this amount of nicotin is not sufficient in the rabbit and rarely in the cat, to paralyze the nerve endings in other muscles of the body." Nicotin, of course, also paralyzes the ciliary ganglion, it being a sympathetic ganglion, as was first shown by Retzius. (It is of interest to note in this connection that a smaller dose of curare is required to paralyze the motor endings in the extrinsic eye muscles, than in other muscles of the body.) Langley and Dickinson (84) found that "the motor nerve-endings are paralyzed in the cat by 10 to 15 m. g. of nicotin, that rather more is required in the rabbit, and considerably more in the dog." The analogy between the action of nicotin and curare is therefore worthy of notice. They both

paralyze the motor nerve-ending in skeletal muscle and both (according to Langley) paralyze the sympathetic cells. They differ in their action in so far that nicotin paralyzes the sympathetic cells more readily than does curare, while curare paralyzes the motor nerve-ending more readily than does nicotin. (Other minor differences need not here be mentioned.) Taking these facts into consideration, it would seem to us more reasonable to say that since curare and nicotin paralyze the *ending* of a motor fiber in skeletal muscle, they paralyze also (reasoning from analogy) the ending of the central, cerebro-spinal fibers in the ganglia, i. e., the end-baskets and not sympathetic nerve cells.

In other words, nicotin and curare paralyze in both instances the end-brush of the cerebro-spinal fiber, which in striated muscle ends under the sarcolemma; in the sympathetic ganglia this end-brush is woven into a basket-like structure, the intra-capsular, peri-cellular basket. Ehrlich (4), in his first communication on the action of methylen-blue on living nerve tissues, draws attention to the similarity in structure between the end-baskets and the ending in voluntary muscle, and adds: "I think these phenomena (resemblance in structure and the fact they both stain readily in methylen-blue) may be of importance to physiology and pharmacology, as it is very probable that the end basket may localize poisons, other than methylen-blue, and may therefore be locally paralyzed like the ending in striated muscle."

By way of summary, I shall reproduce briefly the arguments, which seem to indicate that the central fibers are of cerebro-spinal origin and end in sympathetic ganglia. I shall for this purpose select the ciliary ganglion and the nerves in connection with it.

It is well known that the ciliary ganglion receives fibers from the IIIrd and Vth cranial nerves and probably also sympathetic fibers, and from it the short ciliary nerves, 6 to 10 in number, pass to the ciliary body and iris. Stimulation of the third nerve causes, among other things, closure of the pupil



and contraction of the ciliary body. Direct stimulation of the ganglion and the short ciliary nerves give the same results.

When the ciliary ganglion is stained with the Golgi method, as has been done by Retzius (85), Kölliker (33) and Michel (74), it may be seen that its cells are multipolar, therefore sympathetic neurons, the neuraxes of which extend into the short ciliary nerve, and no doubt innervate the involuntary muscle of the ciliary body and iris. Kölliker (32) and Michel (74) have shown that the cell bodies of these sympathetic neurons are surrounded by peri-cellular baskets. In methylen-blue preparations, I find that these peri-cellular baskets are intracapsular and are the endings of small medullated nerves entering the ganglion.

Langley and Anderson (85) have shown that after the injection of 10 m. g. of nicotin into the vein of a rabbit or cat, stimulation of the third cranial nerve has no effect of any kind, the non-contraction of the extrinsic eye muscle innervated by this nerve, being due to a paralysis of the motor endings, the non-closure of the pupil, to paralysis of the ganglion cells of the ciliary ganglion, or, if our interpretation of the action of nicotin is correct, to a paralysis of the end-baskets of the third nerve in this ganglion. Stimulation of the short ciliary nerves causes closure of the pupil after injection of nicotine which of course would not be the case if the third nerve passed through the ganglion without ending therein. Further proof of the ending of the third nerve in the ciliary ganglion is furnished by Apolant in the following experiments. Apolant divided the third nerve, on one side, in cats, just before it enters the orbital cavity. At the end of two weeks, the contents of the orbit, on the operated and unoperated side were removed and hardened in Müller's fluid. After proper hardening the ciliary ganglia with the third and the branch from the fifth nerve were dissected out and pinned out on elder pith—this to bring the ganglion and its roots into a plane. The preparation was then stained after Marchi's method, embedded and cut into serial sections. Apolant states that on the operated side, the third nerve and its branches were in every instance degener-

ated. The degenerated fibers could be traced to the periphery of the ciliary ganglion but not beyond the ganglion cells, while the short ciliary nerves were never found degenerated. These experiments show very conclusively that these medullated fibers ending in the ciliary ganglion, are the neuraxes of neurons situated central to the point of section. The non-degeneration of the short ciliary branches can only be explained by the fact that they are neuraxes of neurons, the trophic center of which—the cell body and nucleus of the neuron—are situated peripheral to the point of section, namely in the ciliary ganglion. Sections of the ganglion and nerves of the normal side containing no degenerated fibers show however that the fibers entering the ganglion from the third nerve are very small medullated fibers, which can be likened to the central fibers ending in other sympathetic ganglia.

The fibers from the Vth nerve and those from the sympathetic, forming the sensory and sympathetic roots do not end in the ganglion, as may be seen from Langley and Anderson's (83) and from Apolant's (86) work.

Thus far my discussion has been largely concerned with the larger ganglia of the chain and the cranial ganglia, into which the small medullated nerves—central fibers—can be traced without much difficulty.

It must not however be supposed that such nerves end only in these larger ganglia. All evidence we possess goes to show that similar nerves end in all the sympathetic ganglia, even the small terminal ganglia. Attention has already been drawn to the fact that intra-capsular, peri-cellular baskets—the endings of the small medullated, the central or pre-ganglionic fibers—are to be found in even the smallest peripheral or terminal ganglia. This alone would justify the assumption that pre-ganglionic fibers end in the peripheral ganglia. It is however not difficult to show, (and especially in methylene-blue preparations) that small medullated fibers, larger than the medullated fibers of the sympathetic system, enter the small peripheral ganglia and terminate in end-baskets. We must assume then that many of the nerve fibers of the white rami pass

through the ganglia of the chain to the peripheral ganglia, or, at most, give off only collateral branches in the chain-ganglia, the fiber itself going to the periphery, and ending in some ganglion situated at a variable distance from the chain.

Such medullated fibers constitute the white rami of the peripheral ganglia. The central or pre-ganglionic fibers forming such white rami differ only in length, not in structure, from the central or pre-ganglionic fibers ending the ganglia of the chain.

There is reason to believe that a central fiber may end in peri-cellular baskets in more than one ganglion, as Langley (87) has shown and represents in several diagrammatic figures, and as may be seen from Fig. (10) combined and slightly altered from Langley's figures.

In methylen-blue preparations of the sympathetic of the frog, in which only a few fibers ending in baskets were stained, I have several times observed that a medullated fiber—central fiber—giving off one or two side branches, terminating in a spiral and end basket, could be traced beyond the ganglion in which these side branches were given off, into a neighboring ganglion. These observations corroborate to some extent Langley's conclusions arrived at in experiments with nicotine. I have thus far not succeeded in finding spiral fibers and end-baskets on the same medullated fiber in two ganglia, but would think that in suitable preparations such a fiber might be found.

We are prepared, it seems to me, to formulate the following conclusions. The sympathetic neurons, the cell bodies and dendrites of which are grouped to form the sympathetic ganglia, form the terminal link of a nerve or neuron chain, of which the second link is formed by a neuron, the cell body of which is situated in the cerebro-spinal axis and the neuraxis of which leaves the spinal cord or medulla through the anterior or motor root as small medullated fibers, which fibers end in intra-capsular, peri-cellular baskets, enclosing the cell bodies of the terminal—sympathetic—neuron. An impulse issuing from the cord or medulla along the central or pre-ganglionic fibers is transferred to the cell body of a sympathetic neuron and thence along its

neuraxis to some peripheral tissue. Whether all sympathetic neurons are thus connected with the cerebro-spinal system can at present not be positively stated. The evidence is, however, in favor of the supposition that by far the greater majority form the terminal link in such a neuron chain.

The question has no doubt suggested itself to you, whether the neuraxes of sympathetic neurons ever terminate in other sympathetic ganglia, there to stimulate other neurons, or do they always form terminal links in a neuron chain? Langley, in several of his communications, denies the possibility of such an ending. In his (88) short account of the sympathetic system the following statement occurs,—“The ganglia of the sympathetic trunk send no fibers to one another.” This conclusion, if I understand Langley correctly, is based largely on observations made after the injection of nicotin. In certain ganglia, as for instance the superior cervical, local application of nicotin stops all the effects produced by stimulating the cervical sympathetic. In Auerbach's and Meissner's ganglia however, Langley and Anderson (89) have shown that “Large doses of nicotin do not paralyze any of the effects which can be obtained by stimulating the fibers given off by the inferior mesenteric ganglion of the pelvic plexus.” They add: “It is true that in most cases motor effects on the intestine were diminished to a greater extent than inhibitory or vaso-constrictor effects, this difference was however not constant.” They conclude that the connection which exists between the nerves coming to the intestine and the cells of Auerbach's and Meissner's plexus is of a different nature from that which exists between the pre-ganglionic fibers and sympathetic nerve cells in other parts of the sympathetic; and, “That the nerve cells of the plexuses of Auerbach and Meissner do not belong to the cells of the sympathetic but are cells of a different nature.”

Kölliker (34) has already drawn attention to the erroneous-ness of this last conclusion, and Dogiel (55) has shown that in mammalia the cells of Auerbach's and Meissner's plexuses are in shape and structure like the ganglion cells in other sympathetic ganglia. Dogiel (55) has further shown that medullated



fibers, which end in peri-cellular baskets, can be traced, into these ganglia. These observations I can corroborate for the cat and rabbit and also for the reptilia (*Chelydra serpentina*). I have also found peri-cellular baskets; the number has however been relatively small. I should infer that not all the sympathetic neurons of Auerbach's plexus are in connection with medullated fibers through peri-cellular baskets. In frogs and fishes the nerve cells of Auerbach's plexus have often been stained, but so far no peri-cellular baskets have been observed.

The diminution in the motor effect, observed after the injection of nicotin and subsequent stimulation of the fibers given off from the inferior mesenteric ganglia and those of the pelvic plexus, may be due to a paralysis of peri-cellular baskets in Auerbach's and Meissner's plexus. The fact that not all the effects were lost after the injection of nicotin may be explained in one of two ways—(1) Some of the nerve fibers in Auerbach's and Meissner's plexuses may not be connected with nerve cells beyond the inferior mesenteric ganglia, in which case nicotin would not paralyze their action. (2) Some of the neuraxes of the neurons in the inferior mesenteric ganglia may terminate in the peripheral ganglia of Auerbach's and Meissner's plexuses.

I have previously stated that evidence of the ending of neuraxes of sympathetic neurons on the protoplasmic branches of other sympathetic neurons was to be had from a study of thin sections of methylen-blue stained sympathetic ganglia, and that such neuraxes seemed to come from neurons in more centrally located ganglia. The fact that nicotin experiments lead to a contrary conclusion, seems to me to be insufficient evidence on which to base such a conclusion. If we assume that nicotin paralyzes the end baskets, and not the ganglion cells of sympathetic ganglia, it may readily be seen, that, owing to this selective action of nicotin, the endings of the neuraxes of sympathetic neurons on the dendrites of other sympathetic neurons may escape paralysis by nicotin, as the terminations of the neuraxes of sympathetic cells in non-striated or heart muscle or in gland tissue escape paralysis. It would seem

therefore that experiments with nicotin are not suitable for the solution of the question under discussion. It may be said that the evidence seems against the assumption that nicotin paralyzes the endings of the neuraxes of sympathetic neurons, as it does the endings (peri-cellular, intra-capsular baskets) of the central fibers in the sympathetic ganglia. This hypothesis is offered, as a suggestion, to explain certain sympathetic effects which nicotin does not interrupt.

*The grey rami communicantes.*—In a general way it may be stated that each spinal nerve has a grey ramus. Langley (82) states that in the cat the superior cervical ganglion gives off dorsally, from its posterior surface, fibers to the first three spinal nerves; the stellate ganglion sends branches from the IIIrd cervical to the IIIrd or IVth dorsal nerve inclusive. From the Vth dorsal to the first coccygeal, there is usually a sympathetic ganglion and grey ramus corresponding to each spinal nerve.

As has already been shown, structurally a grey ramus consists largely of non-medullated nerve fibers, which, as Gaskell (78) states, are intimately connected with the corresponding lateral ganglion, its nerve fibers being in direct connection with the nerve cells of that ganglion.

Langley (82), Langley and Sherrington (90) have made some very interesting observations on the distribution of the grey rami in two communications dealing with the pilo-motor nerves of the cat and monkey. In their joint publication, they point out that, in the monkey, stimulation of the cervical, and in the cat, stimulation of the lumbar sympathetic causes a contraction of the erectores pilorum in certain definite areas of the skin, thus causing an erection of the hairs in these areas. The nerve fibers going to these muscles are spoken of as pilo-motor nerves.

Langley (82) has found that the pilo-motor fibers run from the spinal cord in the anterior roots of the spinal nerves. And further finds that, "Nicotin annuls the pilo-motor effect of stimulating the roots of the spinal nerves (as it does all the visceral effects), but does not effect the the pilo-motor effect of

stimulating the peripheral nerves. The pilo-motor nerves then (like all visceral nerves) are connected at some point of their course with nerve cells. \* \* \* The pilo-motor nerves in the various rami of the superior cervical ganglion are typically all connected with the nerve cells in this ganglion. The cervical rami of the ganglion stellatum, and the grey rami of the first three thoracic nerves are connected with the nerve cells in the ganglion stellatum. From the Vth thoracic to the VIth lumbar grey ramus inclusive, all the fibers of the grey ramus are, as a rule, connected with the nerve cells in the corresponding ganglion.

It will not be necessary to describe in detail the experiments which have led to the above conclusions, nor to do more than to state that experiments with nicotin show conclusively that the grey rami consist largely of the neuraxes of the sympathetic neurons of the respective ganglia. As to the further course of the pilo-motor nerves in the spinal nerves, Langley has shown: "That so far as the skin is concerned, the distribution of all the sympathetic fibers which run to the spinal nerve (grey rami) is the same as that of the sensory fibers of the nerve, and that the distribution of the sympathetic fibers of a spinal nerve can in the main be determined by dissecting the nerve in its course." The white and gray rami differ therefore in structure and function. The former consist of the small medullated fibers, the neuraxes of neurons of the cerebro-spinal axes, ending in baskets; the latter of the neuraxes of the sympathetic neurons in the ganglia, which become associated with the spinal nerves. They form the terminal link of a neuron chain of which the white rami form a portion of the second link. In the grey rami are found a variable number of medullated fibers, as has been shown by Gaskell, Langley and others. Langley (91) states that their diameter varies from  $2\ \mu$  to  $4\ \mu$  and some fibers above this size 6 to  $12\ \mu$ . Some of the smallest are medullated sympathetic fibers (Kölliker (32) states that the pilo-motor fibers—"Haarbalgmuskeln-Nerven"—of the cat are medullated sympathetic fibers); a few, chiefly the medium sized and larger, come from the posterior

root ganglia; and sometimes a few efferent medullated fibers, passing to the sympathetic ganglia by the white rami, leave the sympathetic ganglia by the grey rami. They are destined to terminate on the aberrant sympathetic cells, lying in the grey rami before they reach the spinal nerves.

*Sensory nerve fibers in the sympathetic.* There seems to be no doubt that sensory nerve fibers—cerebro-spinal fibers—exist in the sympathetic system. Lenhossék (28) has shown that fibers from the sensory roots enter the sympathetic ganglia, also that the sphenopalatine ganglion (sympathetic, Lenhossék) receives a bundle of nerves from the Gasserian ganglion, and further that some of the peripheral fibers of the geniculate ganglion (this ganglion contains "T"-shaped cells like the spinal ganglia, Lenhossék (92)) enter the chorda tympani. Lenhossék inclines to the view that these sensory fibers end in the sympathetic ganglia, presumably in peri-cellular baskets, possibly in free endings. From what has been said concerning the white rami and their endings in the ganglia, it may be seen that the central fibers leave the cord through the anterior root. It would seem therefore that these sensory fibers do not end in the ganglia, which they reach probably through the white rami, but pass through the ganglia of the chain and become associated with the efferent sympathetic nerves. They may in this way pass through a number of sympathetic ganglia before reaching their destination. Such medullated fibers, which are larger than the central or pre-ganglionic fibers, have been traced by me through two and through three of the small ganglia found in the frog's bladder; and in no instance were they seen to give off any branches before terminating. Kölliker and Langley state that these medullated fibers are of variable size. No doubt many of the medium sized and larger medullated fibers found in sympathetic nerves are sensory. As to their mode of ending we have as yet very little positive evidence. Some no doubt end in the Pacinian bodies found in the mesentery and occasionally in the pancreas. The medullated fibers ending in the Pacinian bodies are, judging from the size of their axis-cylinders as seen in methylen-blue



stained preparations, quite large. Other sensory fibers of the sympathetic terminate in free endings. In a number of methylen-blue preparations of the frog's bladder in my possession, such an ending is most clearly shown. In some of the most successful preparations, large medullated fibers can be traced in small nerve trunks, from a point at which such nerve trunks reach the base of the bladder, through several sympathetic ganglia, to their ending. From place to place one or the other of the large medullated fibers, or several such fibers, leave the main trunk and, after traversing a longer or shorter distance, break up into two or three short medullated branches, each consisting of two, three or four short internodal segments. From these short medullated branches, varicose, non-medullated side branches are given off at the nodes of Ranvier, which break up into a large number of finer branches, ending in small bulbous enlargements between the cells of the bladder epithelium. The medullated branches after losing their myelin terminate in the same way. I estimate that a sensory fiber ending in the bladder of the frog supplies an area of about .2-.3 sq. mm. In Fig. 11 is reproduced the ending of a sensory fiber in this organ.

Smirnow (93) has described sensory endings in the heart of amphibia and mammalia; in the latter both in the endocardium and the exo-cardium. The endings are found in the connective tissue of the heart and are the terminal branches of large medullated nerves, which, after giving off side branches, lose their myelin and terminate in an end-brush with terminal bulbar enlargements.

Smirnow has endeavored to ascertain, by degeneration, whether the sensory endings belong to the depressor nerve of the heart. The two experiments, one on the cat and one on the rabbit, in which such degeneration was attempted, gave results which were interpreted as showing that the sensory endings in the heart belonged to this nerve.

I may at this point draw attention to the fact that in our text-books of anatomy it is customary to speak of a sympathetic ganglion as having three roots, a motor, a sensory and a

sympathetic root. I refer here more especially to the sympathetic ganglia in connection with some of the cranial nerves. If we take for instance the ciliary ganglion, to which your attention has previously been drawn, we find it generally stated, that it receives its motor root from the 3rd cranial nerve, its sensory root from the nasal branch of the ophthalmic and its sympathetic root from the cavernous plexus of the sympathetic. I have tried to show you that the motor root, consisting of small medullated fibers, ends in the ganglion in peri-cellular baskets. The sensory root, when viewed in the light of our more modern ideas of the structure of the nervous system has no connection, by that of course is meant no histological connection, with the ganglion. It is doubtful whether the sympathetic root really forms any connection with the ganglion; some of its fibers may end free on the dendrites of the sympathetic neurons constituting the ganglion. Or if we take the so-called sub-maxillary ganglion, Quain states: "The posterior connecting branch from the lingual nerve, often broken up into two or three filaments, conveys to the ganglion fibers from the chorda tympani and inferior maxillary nerves and thus represents the motor and sensory roots of the ganglion. The sympathetic root is formed by slender twigs from the plexus on the facial artery." Langley (94) has shown (by his nicotin method) that some of the chorda tympani fibers end in this ganglion, and I have endeavored to show that such fibers end in peri-cellular baskets. The sensory fibers no doubt pass through the ganglion to end in some of the larger gland ducts. I infer this from the fact that some of the larger medullated fibers pass through the ganglia without ending therein; similar medullated fibers are found by the side of the larger gland ducts. They are no doubt sensory fibers, as some of them end free in the epithelium of the ducts. It may also be stated that Langley finds medullated fibers, 7 to 10  $\mu$  in diameter in the plexus surrounding the sub-maxillary duct. These fibers were seen branching. On general grounds he thinks they are sensory fibers. We have no reason to assume that the fibers of the sympathetic root

end in the sub-maxillary ganglion. They may do this in the manner above described for the ciliary ganglion.

The point I wish to emphasize in the two examples selected for analysis, is this. The motor root *ends in the ganglion*, no doubt in peri-cellular end-baskets. This root constitutes the *white ramus of the ganglion*. The sensory root forms no histological connection with the ganglion, accompanying the efferent sympathetic nerves to the tissues. Whether the sympathetic root ends in the ganglion is questionable, if so, its nerves end on the dendrites of the sympathetic cells and are not paralyzed by the nicotin.

*Reflexes in sympathetic ganglia.*—Attention has previously been called to the possibility of peripheral reflexes, i. e. reflexes in sympathetic ganglia, in speaking of the sensory sympathetic cells described by Dogiel (71). This type of cell, it will be remembered, has long dendrites, which, as Dogiel suggests, may reach to the free surface; the neuraxis ending free in other sympathetic ganglia. A sensory sympathetic neuron, stimulated through its dendrite, might excite through its neuraxis a motor sympathetic neuron, the impulse not going to the cerebro-spinal axis. Langley and Anderson (95) state that two cases of reflex action occurring in peripheral ganglia have been brought forward—reflex from the submaxillary ganglion of the dog (Claude Bernard) and reflex from the inferior mesenteric ganglion of the cat (Sokownin). The apparent existence of recurrent fibers in the lingual nerve makes it difficult to determine with any degree of accuracy the existence of a peripheral reflex in the submaxillary ganglion. For the inferior mesenteric ganglion the existence of a peripheral reflex seems quite clearly established by Langley and Anderson. It would be beyond the scope of these lectures, to reproduce fully the observations, which lead to this conclusion. I may however add that they show: "That the effects which follow the stimulation of the central end of the hypogastric nerves (all nerves going or coming from the inferior mesenteric ganglion, except the hypogastrics having previously been cut) are not due to recurrent fibers, but to fibers, the trophic centers of which are in the

spinal cord." They further conclude that such reflexes are due to motor nerves.

The view which they tentatively express is the following. They suppose that on stimulating a peripheral nerve, the impulse may travel up this peripheral nerve until it reaches a collateral branch (in this case in the inferior mesenteric ganglion), then down the collateral branch, and that this impulse may set up other impulses in the sympathetic nerve cells. The following diagram (Fig. 12), which is slightly modified from one given by Langley (88) in his short account of the sympathetic system, Physiological Congress, Berne, 1895, may serve to illustrate the point in question.

*A* and *A'*, a central (pre-ganglionic) fiber; *B*, a collateral branch; *C* and *D* sympathetic neurons with neuraxes ( $\alpha$ ) ending in the bladder, *Bl*. The central fiber is stimulated at *A'*, the arrows indicate the course the impulse would travel in a peripheral reflex. I am not prepared to make comment on this hypothesis, as suggested by Langley. It would seem well, however, to regard it as tentative until further work, both physiological and histological, corroborates or disproves its accuracy. Possibly the existence of sensory sympathetic cells, the cell bodies of which are located in the inferior mesenteric ganglion, the dendrites of which extend into one of the hypogastric nerves, may be found, in which case a peripheral reflex in this ganglion might take place through such sensory cells.

In closing these lectures, I desire to draw your attention to two diagrams, by means of which I hope to summarize in a graphical way many of the points I have emphasized in these lectures.

These diagrams may serve to show,—(1) the probable arrangement of the spinal nerves in a metameric segment, and their connection with the sympathetic ganglia of the chain, the pre-vertebral ganglia and peripheral ganglia; (2) the probable connection of the nerves concerned in the innervation of the sub-lingual and submaxillary glands.

Fig. 13. Showing the probable arrangement of the neu



rons in a metameric segment. In the construction of this diagram I have been greatly aided by Fig. 840 of Vol. II, Part II, of Kölliker's *Gewebelehre* and also several figures in Vol. III, Part II, of Quain's *Anatomy*.

In the figure *S. C.* represents one half of the spinal cord; *A. R.*, the anterior root; *P. R.*, the posterior root with the spinal ganglion; *P. S. B.*, the posterior branch of the spinal nerve; *L. S. B.*, the lateral or mesial branch of the spinal nerve; *W. R.*, the white ramus; *G. R.*, the grey ramus; *I-II-III C. G.*, three sympathetic ganglia of the chain united by intervening nerves; *Pr. V. G.*, a pre-vertebral ganglion; *Periph. G.*, a peripheral ganglion.

In Fig. 13, the following colors have been used to designate neurons of different orders, and in the following way:—A *black line (m. n.)* designates a motor neuron of the spinal cord, with the cell body in the anterior horn, the end-brush in striated muscle. A *black line crossed by short black dashes (s. n.)*, a sensory spinal neuron of a somatic nerve, ending in the epidermis or in some special sense organ. The cell body of such a neuron is in the posterior root ganglion. An *interrupted black line* denotes a sensory, spinal nerve, accompanying efferent sympathetic fibers to the viscera (*s. s. f.*). Such fibers, it is assumed, come from cells in the posterior root ganglion, pass to the sympathetic ganglia through the white rami, and through the several sympathetic ganglia until they reach the periphery, there to end either in a free ending (*s. s. f. (1)*), or in a Pacinian corpuscle (*s. s. f. (2)*). The neurons *colored blue*, are the pre-ganglionic fibers of Langley or the 'central fibers'. I have followed Fig. 240, of Quain's *Anatomy*, Vol. III, Pt. II, in placing the cell bodies of such neurons in the lateral portion of the anterior horn of the spinal cord. The neuraxes of such cells leave the spinal cord through the anterior horn, and reach the sympathetic ganglia through the white rami (*W. R.*), where they terminate in peri-cellular baskets, enclosing the cell bodies of the sympathetic neurons (red in the figure).

The pre-ganglionic fibers leaving the anterior root and the

white ramus of a segment may terminate in one of the following ways.

In the figure, *a* shows a pre-ganglionic fiber which passes through the chain ganglion of the segment (I C. G.), to terminate in the next higher chain ganglion (III C. G.); *b*, a pre-ganglionic fiber passing through the chain ganglion of the segment to terminate in the next lower chain ganglion (II C. G.); *c*, two pre-ganglionic fibers ending in the chain ganglion of the segment; *d*, a pre-ganglionic fiber passing through the chain ganglion and ending in a pre-vertebral ganglion (*Pr. V. G.*) (this fiber may represent one of the fibers of a splanchnic nerve); *e*, a pre-ganglionic fiber passing through the ganglion of the chain, through a pre-vertebral ganglion to end in a peripheral ganglion; *f*, a pre-ganglionic fiber, which gives a collateral branch in one ganglion (terminating in a peri-cellular basket), and passes on to terminate in some more peripheral ganglion. The ganglion of each segment, probably receives pre-ganglionic fibers from the adjacent higher and lower ganglion, designated by the letters *g* and *h* in the figure.

The sympathetic neurons are colored red in the figure. The cell bodies of such neurons are enclosed in peri-cellular baskets (see figure). The neuraxes of the sympathetic neurons may terminate, either in blood-vessels—vaso-motor—*i*, of the figure; in the involuntary muscle of the viscera—motor—*j*, of the figure; in heart muscle, not shown in the figure; in glands—secretory fibers—*k*, of the figure, or in the sympathetic ganglion (?), *l*, of the figure.

The diagram shows, further, two sensory neurons (Dogiel) one in a peripheral ganglion, *o*; the other in the chain ganglion, *p*, its neuraxis ending in the spinal ganglion in a peri-cellular basket, enclosing the cell body of a 'type two' spinal ganglion cell (Dogiel), *q*, in the figure. Fig. 14 shows the nerve supply of the sub-lingual and sub-maxillary glands. In this figure the several colors used in Fig. 13, and there described, are again made use of. *Sub. max.*, a portion of the sub-maxillary gland with its duct. *Sub. ling.*, a portion of the sub-lingual gland with its duct. *Ch. T.*, the chorda tympani. *Ling.*, the lingual

nerve. *Gen. G.*, a cell of the geniculate ganglion. *Ch. L. T.*, the chorda-lingual triangle (Langley), formed by the chorda tympani, the lingual nerve and the sub-maxillary duct. This triangle contains the sub-lingual ganglion (*Sub. l. G.*). *Sub. m. G.*, the sub-maxillary ganglion in the hilum of the sub-maxillary gland. *Sup. c. G.*, superior cervical ganglion; *Cerv. S.*, cervical sympathetic; *Inf. c. G.*, inferior cervical ganglion; *An. V.*, Annulus of Vieussens; *St. G.*, the stellate ganglion; *Symp. c.*, a portion of the sympathetic chain, *sp. c.*, a portion of the dorsal spinal cord with II, III, IV; *Dr. n.*, the second, third and fourth spinal nerves; *W. R.*, the white rami coming from these spinal nerves.

The nerve fibers of the lingual nerve (*ling.*) are diagramed in black. The figures show its neurons to be sensory. The cells of the geniculate ganglion are also sensory (Lenhossék). The nerve fibers coming from these cells join the chorda (*ch. T.*) and terminate in a free ending on the ducts of the sub-maxillary gland (probably also in the sub-lingual gland).

The fibers in the chorda tympani (*ch. T.*) colored blue in the figure, are comparable to the fibers of the white rami. Some end in peri-cellular baskets in the sublingual ganglion (*sub. l. G.*), others accompany the sub-maxillary duct to the hilum of the gland, where they end in peri-cellular baskets.

The sympathetic neurons of the sub-lingual ganglion (*sub. l. G.*) and of the sub-maxillary ganglion (*sub. m. G.*) are colored red. The neuraxes of the sympathetic neurons of the sub-lingual ganglion accompany the ducts of the gland and end on the secreting cells. The neuraxes of the sympathetic cells of the sub-maxillary ganglion (*sub. m. G.*) accompany the sub-maxillary gland ducts and end on its secreting cells.

The secretory fibers from the spinal cord leave the cord through the anterior roots of the II, III, IV dorsal nerves; through their white rami (*W. R.*) they reach the stellate ganglion, (*St. G.*). They pass through this ganglion, through the annulus (*An. V.*), through the inferior cervical ganglion (*Inf. c. G.*), and by way of the cervical sympathetic they reach the superior cervical ganglion, (*Sup. c. G.*), and end in peri-cellular

baskets enclosing the cell-bodies of sympathetic neurons, (colored red in figure), the neuraxes of which (*symp. n. g.*) follow the blood-vessels to the sub-maxillary, and probably also to the sub-lingual gland. Their mode of ending is not known.

Finally, in closing these lectures, may I again emphasize the fact that at least the great majority of the sympathetic neurons form terminal links in a neuron chain, of which the second link is formed by the fibers constituting the white rami. I trust therefore that the statement that the entire nervous system is a unit, of which the sympathetic system is of necessity only a part, may have become to you a demonstrated fact, and that in your future work you will regard it as such.

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## DESCRIPTION OF PLATES.

## PLATE VIII.

*Fig. 1.* Small sympathetic ganglion in the wall of the trachea, stained in methylen-blue. (Arnstein (36) Fig. 8)

*A*, sympathetic cell; *a*, neuraxis; *b*, dendritēs; *c*, involuntary muscle tissue. *Pr. G. F.*, preganglionic fiber; *Pr. B.*, pericellular baskets.

*Fig. 2.* Ending of non-medullated nerve fiber, neuraxis of sympathetic neuron, in involuntary muscle cell of the intestine of a cat. 1-12 in. oil immersion obj., Leitz, and No. 1 eye piece. From section of  $5\mu$  thickness, double stained in methylen-blue and alum carmine; *a*, neuraxis of sympathetic neuron, ending on cell *b*, at *a'*; *c*, nucleus of cell.

*Fig. 3.* Showing vaso-motor nerves of a small vessel in pharynx of frog, stained in methylen-blue. Leitz 1-12 in. oil im., No. 1 eye-piece. A few of the non-striated muscle cells of the vessel wall were stained, as shown in the figure.

*Fig. 4.* Ending of the neuraxes of sympathetic neurons on the heart-muscle cells of a cat's auricle; from sections double stained in methylen-blue and alum carmine. The figure shows endings of varying complexity: *a*, a very simple ending; *b* and *c*, more complex endings. Leitz 1-12 oil im., No. 1 eye piece.

*Fig. 5.* Ending of sympathetic nerves on gland cells. Copied from Arnstein (61):—

*a*, isolated gland cell from the parotid gland of a rabbit;

*b*, isolated gland cells from the mammary gland of a pregnant cat;

*c*, isolated gland cell from a sweat gland;

*d*, a portion of a teased sweat gland, showing a number of cells with nerve endings.

*Fig. 6.* Scheme of reflex in the sympathetic ganglia in the intestinal plexus. Copied from Dogiel (71).

*a*, motor sympathetic neurons; *b*, a sensory sympathetic neuron; *pr*, dendrites or protoplasmic branches; *ax*, axis-cylinder branches or neuraxes.

1, tunica propria; 2, muscularis mucosa; 3, submucosa; 4, muscular coat with four sympathetic ganglia.

*Fig. 7.* From section of sympathetic ganglion (semilunar) of a cat, stained in methylen-blue. Leitz 1-12 in. im. No. 1 eye piece, reduced to two-thirds.

*a*, cell body of sympathetic neuron; *c*, dendrite; *d*, neuraxis; *b*, neuraxis of another sympathetic neuron ending on dendrite at *b'*.

*Fig. 8.* Sympathetic cells and pericellular baskets from sympathetic ganglia of vertebrates:—

*A*, mammal, (dog); *B*, bird, (chicken); *C* and *C'*, reptilia, (*Chelhydra serpentina*); *D*, frog, (*Rana Catesbiana*); *E*, fish, (*Micropterus dolomieu* Raf).

*a*, neuraxis of a pre-ganglionic fiber, a cerebro-spinal fiber ending in a pericellular basket enclosing the cell body of a sympathetic neuron (*b*); *c*, capsule of sympathetic cells.

Sketches made from ganglia stained in methylen-blue and alum carmine. Camera lucida drawings under 1-12 in. oil im., No. 1 eye-piece, Leitz.

*Fig. 9.* Sketch of the course of a pre-ganglionic, a cerebro-spinal fiber in sympathetic ganglia of a frog. Camera lucida drawing, 1-12 in. oil im., No. 1, eye-piece, reduced to two-fifteenths.

*A*, a medullated cerebro-spinal fiber, which entered the ganglion through a white ramus. An *x* in the course of the fibers indicates a node of Ranvier; the fibers become non-medullated at *y*; *a*, peri-cellular baskets and spirals.

*Fig. 10.* Showing the ending of a pre-ganglionic fiber in more than one ganglion. Copied and slightly altered from two of Langley's (87) figures.

*Sp. c.*, cell in spinal cord; *Ch. G.*, chain ganglion; *S. G.*, solar ganglion; *Pr. G.*, peripheral ganglion.

*A, A', A''*, pre-ganglionic fiber with branches; *a*, neuraxis of sympathetic neurons.

*Fig. 11.* See Plate IX.

*Fig. 12.* Scheme to show how a reflex may occur in the sympathetic system, taken from Langley's (88) account. For description see the text.

#### PLATE IX.

*Fig. 11.* Ending of a sensory neuron in the bladder of a frog. Methylen-blue stained preparation. Camera lucida drawing, 1-12 in. oil im., No. 1 eye-piece. Drawing reduced three times.

*A*, medullated nerve fiber. An *x* indicates a node of Ranvier; *y*, a non-medullated collateral or terminal branch ending in an end-brush.

#### PLATE X.

*Fig. 13.* Diagrammatic representation of the distribution of the spinal and sympathetic neurons in a metameric segment of the cord.

For description see the text.

#### PLATE XI.

*Fig. 14.* Diagram to show the course and connection of the neurons innervating the sublingual and submaxillary glands.

For the description see text.

PRELIMINARY NOTICE UPON THE CYTOLOGY OF  
THE BRAINS OF SOME AMPHIBIANS:

I. NECTURUS.<sup>1</sup>

By SMITH ELY JELLIFFE, M.D.

*With Plates XII and XIII.*

In view of the great impulse which has been given to cytological work within recent years, the writer has felt that a study of the cells of the brains of some of the lower animal forms might give a clue to the correct interpretation of results obtained with human material both normal and diseased.

The study of the nerve cells by means of the methylene blue stain (Nissl) has suggested a number of problems with far-reaching results. The past few years have seen a large accession of workers using this method and the question, as the writer sees it, resolves itself into one of interpretation. Is it true that the physico-chemical changes taking place in nerve cells are accompanied by constant changes in molar composition as Nissl claims? Can these changes be registered and studied by technical microscopical methods as outlined by Hodge, Vas, Mann and numerous others; and finally is the Nissl method or its modifications such a method, and can its pictures be relied upon to give accurate and trustworthy results? Such a broad outline is, however, manifestly beyond the purpose of the present paper which will simply state some points of possible interest obtained thus far in a research which the writer will hardly be able to complete for the present.

For a number of years it has been known that many cells

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<sup>1</sup> The writer wishes to express here his thanks to Professors Osborn and Wilson for their many courtesies and to Dr. Strong for his aid and advice while working in the laboratory.

in the central nervous system of vertebrates, especially the motor cells in the ventral columns of the cord and those in the nuclei of origin of motor nerves, possess a characteristic structure in the presence of what has been termed the chromophilic granules. In general these granules may be described as elongated rod-like, tetrahedronal or irregular portions of protoplasm apparently situated in all parts of the cytoplasm, including the dendrites. In the majority of the cases they seem to occupy the periphery of the cell (cytoplasm) and appear to be arranged in no definite way save perhaps somewhat elongated in the direction of a contiguous dendrite or circularly about the nucleus.

These granules possess marked chemical affinities for certain dyes of the indo-phenol series, notably, methylene, thionine and toluiden blue, though they can be demonstrated by a number of coloring agents. A great variety in the number, shape, size and arrangement has already been described and it becomes a matter of importance to arrive at some definite conceptions regarding them or the cells in which they are found.

The phylogenetic mode of approach has seemed the one which might give the truest answer to this question and the brains of the Amphibia have first been chosen for study. *Menopoma*, *Diemyctylus* and *Rana* have been studied casually, but *Necturus* was chosen as the basis of the following outline.

If this animal represents a retrograde form in a permanent larval condition, it should give pictures of extreme simplicity and the origins of some of the higher types of nerve cells might be here found.

#### METHODS.

It may be a matter of tedious annoyance to have to detail the methods by which any results have been attained, yet such is the great amount of technical refinement that it is necessary.

Several preliminary experiments were made with the view of determining the action of different fixing agents. These experiments were first made upon the cord of *Necturus*, but as this was so small the cord of the cat was finally chosen. Immediately after death the cord was laid bare and a small piece



of uniform calibre was taken from the cervical region. This was cut into seven nearly equal segments and immediately placed in the following hardening fluids:

- (1) Sat. alcoholic solut. corrosive sublimate.
- (2) Absolute alcohol.
- (3) Alcohol 95%.
- (4) Alcohol 95%, formalin 20%, equal vols.
- (5) Formalin 20%.
- (6) Hermann's fluid.
- (7) Flemming's fluid.

In (1), (6) and (7) the pieces remained one hour; in the others, 24.

The pieces were properly identified and then run up into paraffine and blocked, all passing through exactly the same after-treatment in the same vessel, all blocked in the same block, cut at the same stroke of the knife and transferred to the slide, fixed (Mayer) and stained upon the slide. Thus the technique in each series was uniform and similar, excepting the hardening fluid used and the length of time of hardening.

Staining was done by a variety of methods and numerous modifications of the Nissl method were tried. Finally the specimens were mounted in different media, on one slide five specimens of *Necturus* cord were stained under the same conditions and mounted in different media: Xylol Balsam, Xylol Damar, Xylol Colophonium, Nissl's Benzine Colophonium, Chloroform Styra.

The tedium of technique approaches its zenith when one takes up the question of staining. An investigator may say "Nissl's" method, but which one is meant? Nissl has described so many that it is hard to know which is followed and although the variations are slight they are of importance to the original describer at least, and who should be more competent to judge? Hence it may be said that in the experiments made all of Nissl's methods, Rehms' modification, etc., were tried, including the latest described at the time of publication. The method giving apparently the most uniform and clear results, was, substantially, staining in warm  $\frac{1}{2}$  % aq. solut. methylene blue for from 15 to 20

minutes, decolorizing by Nissl's decolorizer or by 95% and absolute alcohol which gave precisely the same pictures.

Thionine blue as recommended by Lenhossék was tried and, while it stains very intensely, the writer found it difficult to deal with.

These experiments seem to show the following :

1. With reference to gross changes due to fixing agents : In the illustrations, six cross sections are figured, which show for themselves. As far as could be made out, absolute alcohol, 95% alcohol and alcohol sublimate acted in almost exactly the same manner ; distortion and contraction were great and seemingly evenly distributed in the grey and the white matter. With equal volumes of 20% formalin and 95% alcohol, the distortion and contraction was much lessened, while formalin 20% was almost like the normal cord. With Hermann's and Flemming's solutions, the contraction was extreme, the gray matter seemingly more strongly acted upon. Thus if external form alone would be the guide, formalin 20% gives the best preservation.

2. In looking upon the effect upon the ganglion cells and their minute structure, a different state of things is shown, the correct interpretation of which would seem to be an extremely difficult matter. In the first place, one can not get the body of the same ganglion cell under these various conditions, which, perhaps in a hypercritical sense, vitiates the results ; then the various angles at which a cell may be cut should be taken into account ; but taking the ganglion cells as they run and choosing those of the larger so-called motor type of the ventral horns, the following conclusions seem warranted by the experiments made.

Between alcohol 95%, and sat. alcoholic sol. of corros. sub. I could detect no essential points of difference. With absol. alcohol, the differences made out were very slight, the pictures being of greater definiteness and sharpness than with the former two reagents. In all three there is contraction of the body of the ganglion cells but as the rest of the cord contracts about

in the same ratio there are no empty spaces left about the cell body.

In the specimens fixed with alcohol-formalin one is struck at first sight by the variation in the staining, these sections taking up methylene blue as well as thionine blue quite strongly, more so than the preceding. In the ganglion cells the body is separated from the surrounding structures slightly; whether this is due to its contraction or the contraction of the surrounding tissues away from it, could not be definitely determined. The granules are slightly indistinct, poorer than with specimens preserved with absolute alcohol. With formalin 20% the staining was even more intense than with the preceding and the contraction of or away from the ganglion cell body was marked. Yet the chromophilic granules came out distinctly. Fixation with Hermann's fluid gave the worst results. The contraction was uniform throughout but the granular structure was irregular, lumpy or broken up into fine granular masses. Flemming's fluid gave better results, the chromophilic granules being often quite sharp and well preserved; contraction was marked, as with the Hermann's.

Thus alcohol 95% and sat. alcoholic sol. of corrosive sublimate gave the sharpest pictures.

As to the use of thionine blue, instead of methylene blue, the comparisons made were in favor of the methylene blue.

With reference to the mounting media, I cannot feel that there is much preference to be shown. Nissl highly recommended benzine colophonium but in the experiments made I could not say that I could detect any differences in the media used, and on submission of the slides to Dr. Strong he could not tell that there was any difference. Perhaps after a lapse of some time there may be differences. Benzine colophonium dries very rapidly and hence may have an advantage in the long run, but after a lapse now of twelve months, the specimens still look alike to my eyes. If I were to express any preference it would be for xylol damar, not on account of its being better but the clearness of the resin is pleasant. Many of my benz. coloph. specimens were of no value at the end of six months. Chlor-

oform styrax from the liquidambar seems a promising medium as it brings out quite sharply the chromophilic granules. Its high refractive index should be born in mind.

#### DESCRIPTION OF THE CELL STRUCTURES OF NECTURUS.

*Spinal Cord.*—All of the cells are clustered about the central canal which is bordered by two or three rows of ependyma cells whose nuclei alone are stained. These measure .075 mm. in diameter; nucleus .003 mm. in diameter. Around these cells is an irregular mass of nuclei which collectively approximate a winged appearance. At the angles of the wing, or, if homologous, the horns, especially the ventral horns, there is a collection of larger cells, the nuclei in these being twice the diameter of the others. Some of these are provided with a faint fringe of blue staining cytoplasm about the nucleus but in none of the specimens examined were there any distinct traces of chromophilic granules.

The rest of the nuclei (cells) have about the same diameter and show an intricate reticulate structure, as do those clustered about the central canal.

*Medulla.*—Passing into the medulla, no changes of note were seen.

At about the level of the glosso-pharyngeal nucleus a number of larger triangular pyramidal cells was seen. These averaged about .035 mm. in diameter, and showed indistinct chromophilic granules of an irregular character, some of which radiated out in the direction of what would appear to be dendrites.

The larger cells making up what appeared to be the motor nucleus of the VII nerve were of much the same character; they averaged .04 mm. and their nuclei were large—,037 mm. In these, faint irregular groupings of stained material approximating the typical chromophilic granules were to be made out.

The motor nucleus of the V nerve showed analogous conditions; here the ganglion cells averaged slightly smaller.

Passing into the *mesencephalon* at about the level of Kingsbury's commiss. optici tecti a number of larger cells were found of peculiar shape. These were more or less square in general ap-



pearance and showed a faint yet distinct protoplasmic covering. They averaged about .03 mm. in diameter, the nucleus being .02 mm. In the cytoplasm were a number of thin streaked masses of colored material quite unlike, however, the typical chromophilic granules. What these "cells" are, I am somewhat at a loss to determine. Throughout their distribution, they remain dorsal and extend slightly laterad being mingled with cells of the regular spinal type. In no cases were any of these cells around the central canal.

The cells of the hypophysis are similar to the regular type; like free nuclei.

Just before reaching the epiphysis there is a sinking in of the cerebral mass, the above mentioned "cells" have practically disappeared, and there was noted the gradual appearance of a dorsal group of large cells in the median line; these vary from .008 to .010 mm.

These do not appear to coalesce with the elliptical ependyma cells which average 17-22 micra in length by 10-16 micra in diameter. At this level the cells around the ventricle are from 8 to 10 rows deep and of the regular spherical free nuclei type, although at rare intervals some cells are seen in which the cytoplasm has responded to the stain, but no granules were found. The cells of the hemispheres were all around the ventricle and were all of the conventional type as were also the cells of the rhinencephalon.

At the time of the final revision the article of Guiseppe Levi, "*Ricerche citologiche comparate sulla cellula nervosa dei vertebrati*," *Rivista di patologia nervosa e mentale*, 1897, 5., is received and some of his results were deemed of importance for the present communication. Among Amphibia the author studied *Rana* and *Bufo* of the *Anura*, *Triton cristatus*, *Spelerpes fuscus* and *Proteus auguinus* of the *Urodeles*; these latter are of more interest from the present point of comparison.

The cells of the ventral columns of the cord have an oval form, the cytoplasm in *Spelerpes* forming a delicate border about the nucleus. In the *Triton* this is more distinct and contains chromophilic granules which were sharply cut, sometimes

fused and all lying in the direction of the principal dendrite. The nucleus is oval, has a delicate acidophile membrane and contains a mass of acidophile granules.

*Dorsal cells of medulla*.—The cytoplasm of Triton is sparse. In Spelerpes and Proteus it is not distinguishable; nucleoli are absent in all.

*Cells of the Pallium*.—No cytoplasm was observed in these cells. The nuclei were oval. The granular olfactory cells were lacking in cytoplasm; the nuclei were oval. In the optic lobes three types of cells were noted: (1) granules similar to those of the olfactory lobes; (2) granules larger than these and richer in basophilic substances; (3) cells with comparatively abundant cytoplasm and containing fused chromophilic granules. These have dark nuclei, which in Triton contain basophilic granules and a homogeneous acidophile substance studded with basophilic granules and in all a nucleolus of the usual character.

Ependyma cells in all contained abundant cytoplasm. The Italian author has not studied these brains from the same point of view as that of the present writer, hence a correlation of the results is somewhat difficult. From the standpoint of cytoplasmic development Spelerpes would represent the most primitive type studied. This would seem to be more primitive even than Necturus, but for the reasons above stated it would be premature to draw any conclusions.

In Necturus we find a predominant type of nerve cells which are indicative of a low grade of development. The chromophilic granules are found in only a few of the cells and when found are elementary or fragmentary in their construction, those of the 7th nucleus appear to be the best developed. The absence of any chromophilic granules in the cells of the pallium is of interest. In Necturus, the chromophilic granules, especially those found in the 7th nerve nucleus, appear to be fibrillar in structure.

Levi's investigations show a similar condition in the pallia of Spelerpes, Triton and Proteus, while in Rana and Bufo a small amount of cytoplasm is found collected in a small conical mass lying to one side of the nucleus, generally the outer side.

The method of staining is, in the author's experience, too restricted, for while it brings out the basophilic structures, the neutrophilic and acidophilic relationships of the different protoplasmic portions of the cell body and nucleus are not shown. Following Flemming, Benda and Levi the compound tinctures might be used to better advantage in the study of the normal nerve cells and further in diseased tissues.

Zoological Laboratory, Columbia University, Jan., 1897.

#### EXPLANATION OF FIGURES.

##### PLATE XII.

- Fig. 1.* Cross section of cord of *Necturus*.
- Fig. 2.* Nucleus of ependyma cell.
- Fig. 3.* Cell in cord about level of the 11th or 12th N.
- Fig. 4.* Nucleus of nerve cells of predominant type.
- Fig. 5.* Cross section of medulla, 10th N. ?
- Fig. 6.* Cell of 7th N. nucleus.
- Fig. 7.* Cross section of mesencephalon.
- Fig. 8.* Nerve cell of mesencephalon.

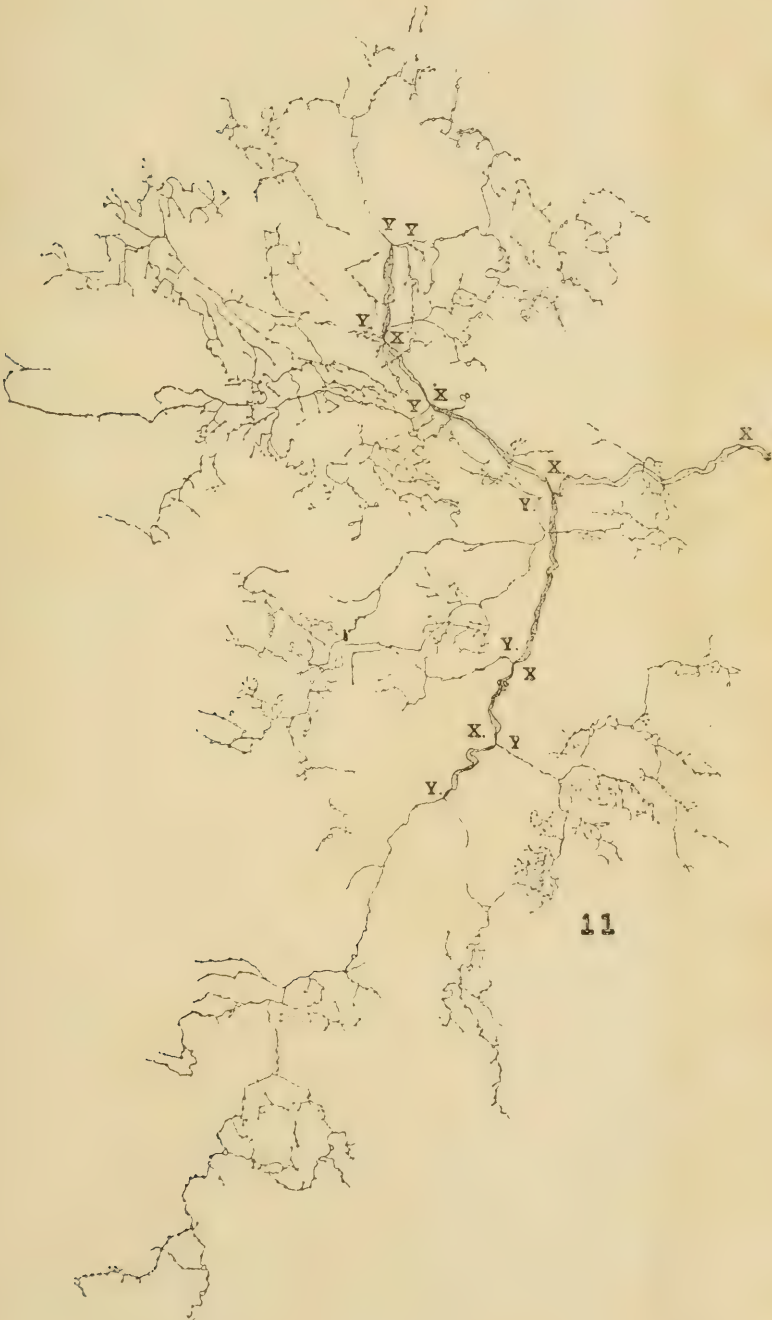
##### PLATE XIII.

- Fig. A.* Cross section cat's cord. Normal size. Cervical.
- Fig. B.* Fixation, alcohol 95%, formalin 20%; equal parts.
- Fig. C.* Fixation, alcohol, 95%; also alc. sat. solut. corrosive sublimate.
- Fig. D.* Fixation, formalin, 20%.
- Fig. E.* Fixation, absolute alcohol.
- Fig. F.* Fixation, Flemming's and Hermann's solutions.







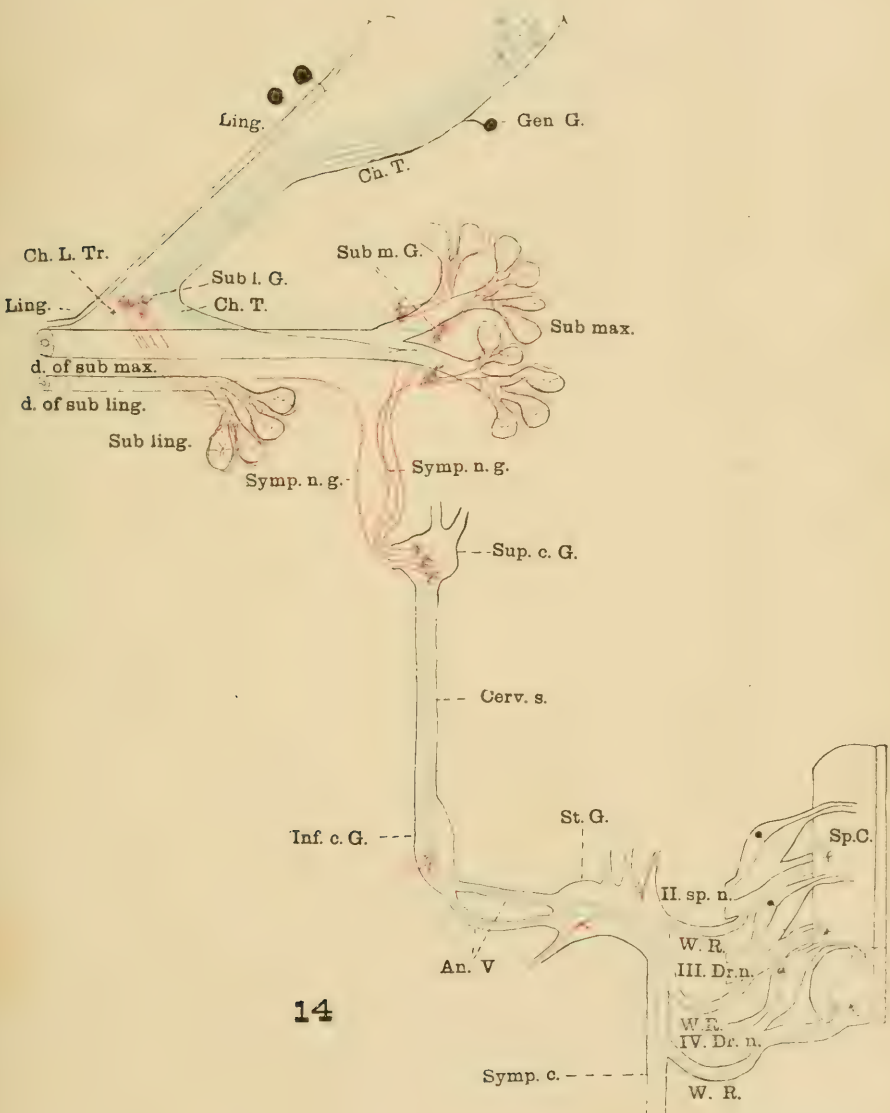




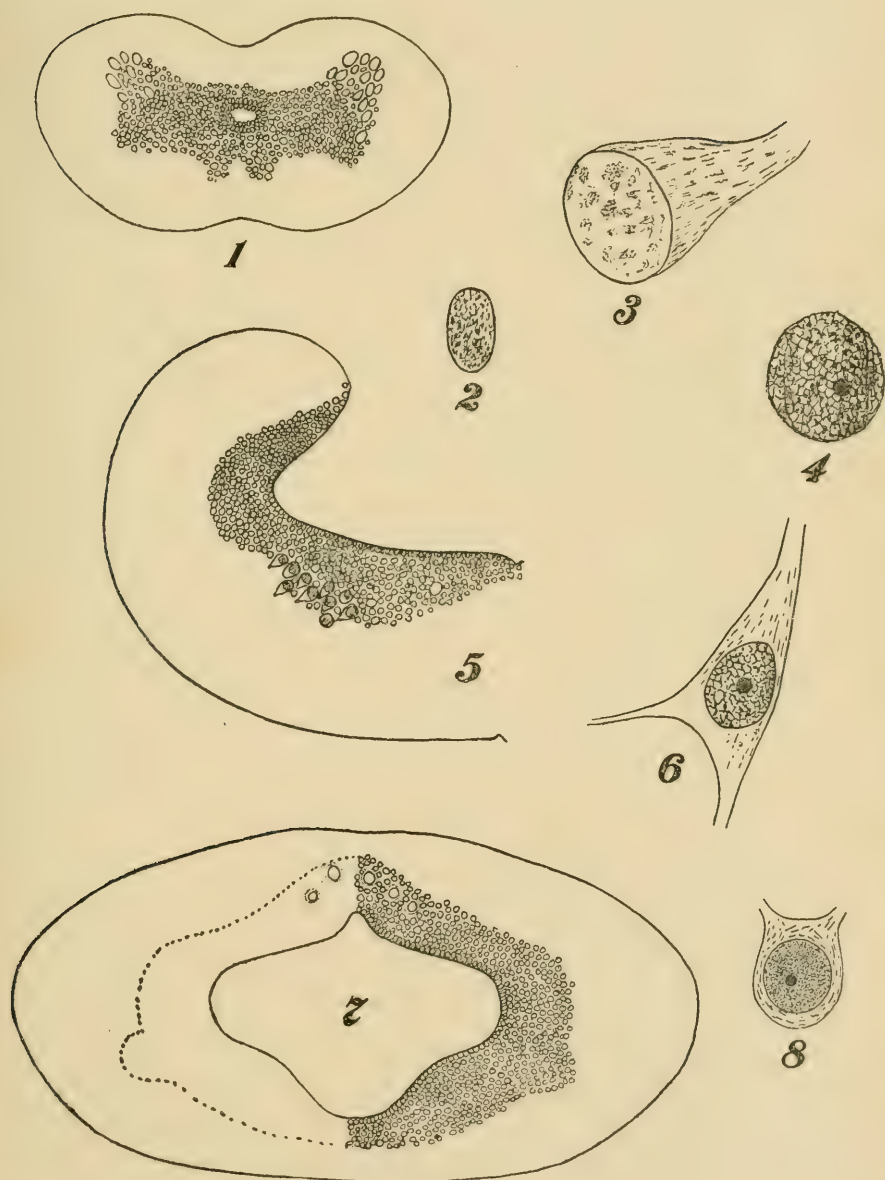






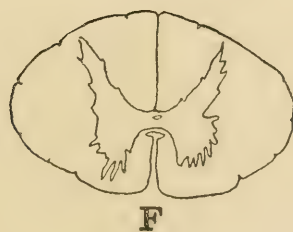
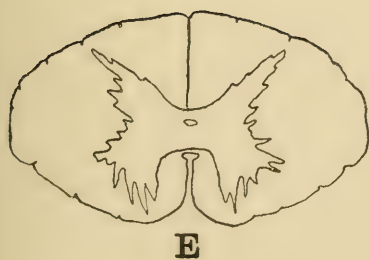
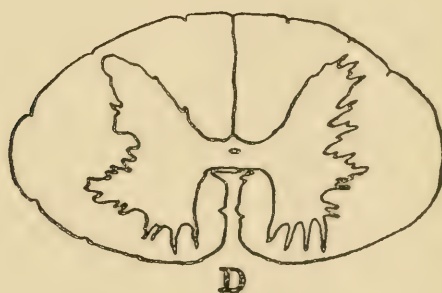
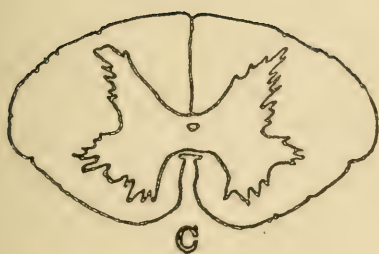
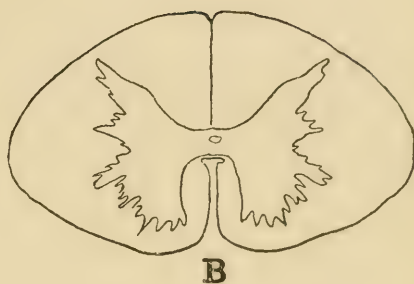
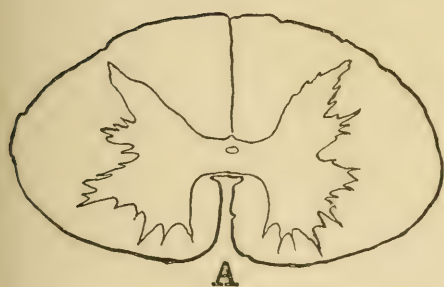














## PSYCHOLOGICAL COROLLARIES OF MODERN NEUROLOGICAL DISCOVERIES.

By C. L. HERRICK.

*An Organ of Consciousness.* The search for the organ of consciousness has remained unfruitful by reason of the total disparity between the conscious and any conceivable form of purely neural activity. Nevertheless it is plain that some sort of neurosis does, in every case, form the immediate preliminary to consciousness, and it is equally clear that not every sort of nervous excitation is an adequate occasion for the emergence of consciousness. The metaphysical nature as well as the peculiar unity and continuity of consciousness has militated against the idea of localizing this power and has disposed to a dynamic view, viz., that the condition of consciousness is not topographical but consists in the form of *activity*.

It is plain that, in the nature of the case, it is impossible to discover a specific portion or a definite *kind* of matter in which consciousness resides, for no complexity of the material unit could make intelligible the diversity in consciousness, while *any* complexity destroys the objective grounds of unity. It is equally hard to discover any physiological basis for the continuity of consciousness. The idea of consciousness as a property is accordingly abandoned and it remains to conceive of it as a *form of energy*. Pure energy with the attribute of spontaneity it could only be if it were in the mode of absolute equilibrium, in which its activities should be wholly reflected into themselves. This can only be predicated of infinite essence and it is necessary to substitute the conditions of *relative* equilibrium in a sphere of interfering activities. The last few years have revealed in the cerebrum a mechanism of neural equilibration of unsuspected complexity, and all that we have recently learned of the physiology of the nerve stimulus only emphasizes the



belief that the whole of the cortical complex is adapted to react as a unit, though not as an invariable unit. The great extent of the system of associational tracts and the facility with which new channels of overflow are set up or marked out is additional evidence in favor of an equilibrium theory of consciousness such as has been advocated by the writer for several years. In this view, the conditions of consciousness consist in the proper equilibration of stimuli to produce a reflection of the stimuli upon the complex of which they form a part. The mechanism of this condition is found in the cortical centres, which are in continual action in such a way that a vortex of activity is in continual flux—each element contributing to the balance of the whole. To this complex external stimuli are continually being admitted, whether as separately unobserved elements from the general-sensation apparatus of the common sensorium (giving rise simply to the implicate concept of personal existence in space), or more specific stimuli through the avenues of the special sense organs. Every sense-content with its escort of reflexly-produced associated elements causes a more or less profound disturbance of the psychical equilibrium and the nature of this disturbance depends not alone on the intensity and state of concentration, but very largely upon the kind of equilibrium already existing. In no case is it possible for consciousness to be double or for more than one conscious act to occur at a time.

It is believed that by the employment of the equilibrium theory we may reach as clear an idea of the conditions and limitations of consciousness as the nature of the case could warrant us in expecting. The character of the conscious act (and the elements of consciousness are always acts) will of course depend upon the extent to which the several factors in the associational system participate in the equilibration. Each disturbance of equilibrium spreads from the point of impact in such a way that progressively more of the possible reflex currents enter the complex, thus producing the extension from mere sensation to the higher processes of apperceptive association. A conscious act is always a fluctuation of equilibrium, so that all

cognitive elements are awakened in response to changes rather than invariable or monotonous stimuli. This conception is not at all opposed to a very complete localization of function, while it nevertheless also applies to the numerous cases of substitutional or vicarious function. It also explains the fact that the loss of a considerable amount of brain substance, in particular within the cortex, is followed by a degradation of the totality of the conscious power.

*Neural Interpolation.* An interesting corollary of the above theory affords an explanation of the phenomena of reproduction. It is a fact which can no longer be doubted that in a number of places in the central nervous system there are formed temporary or permanent clusters of cells whose function it is to proliferate in later periods and thus take the place of the original germinative areas of ventricular epithelium. An interesting analogy exists between this process and the method by which the continual formation of blood corpuscles in later life is provided for. The primitive process of transforming the hæmatoblasts into the definitive corpuscles in various parts of the body becomes progressively restricted by the differentiation of the exposed parts until it is only in a few remnants of the proliferating substrate, as in the red marrow and the so-called blood glands, that the proliferation is usually to be detected. In like manner the original power, common to the embryonic ventricular epithelium throughout its entire extent, of proliferating new neuroblasts is gradually destroyed by the differentiation of the definitive epithelial lining of the ventricles and the proliferating power is inherited by such special outgrowths from the primitive epithelium as have in the mean time lodged themselves in localities suited to their function of perpetuating the structure of the organ and preserving the power of plastic repair and neural substitution. Professor His first showed how such a process is possible by tracing the origin of the olives and nuclei of the medulla. The writer followed with the description of the process in the cerebellum. It was shown in the case of the cerebellum that the essential elements of this massive organ are derived from the ventricular epithelium, to

be sure, but not by a direct migration to their ultimate site, but rather by the formation of germinative areas at the tip and sides of the organ whence, by a species of migration, they reached the entire ectal surface, there to multiply by mitosis until the requisite supply had been produced. (*Jour. Comp. Neurol.* Vol. I, No. 1.) In other papers (*Wood's Ref. Handbook*, Suppl.) the further process was followed until the newly formed cells, sinking below the surface and still continuing to proliferate, reach their permanent places. Though these discoveries were treated contemptuously by certain critics, they have been re-affirmed and verified by a number of independent observers. The writer has also suggested a somewhat similar process for the cells of the cerebrum and, while the details of the process remain to be worked out, there seems to be no doubt that there is a similar segregation of proliferating areas or germinal masses which remain up to a late period capable of producing new cells to be interpolated in the cortical series.

This gives rise to a means for construing the otherwise inexplicable fact that, although the neurocytes are continually degenerating and disappearing, the essential elements of memory remain unchanged. If consciousness consisted in the reactions of various cells or groups of cells, then there would be a footing for the conventional theory of reproduction as a revival of vestiges in the several cells previously affected. But from the equilibrium theory it appears that the state of equilibrium is the important thing, whether that state be the result of the participation of one set of elements or of another whose neural resultant would be the same. Thus, while certain cells of a given cortical complex are disappearing, other cells are entering it and gradually assuming the exact organic constitution adapted to complete their participation in the activity of that complex. By such a process of gradual assimilation and of substitution we conceive that the persistence of memory is to be explained. Still further it seems plain that what we now know of the gradual loss of the finer processes of the dendrites etc., stands in harmony with the observed fact that the earlier, less highly correlated, memories are the last to be lost.



*The Summation-Irradiation Theory of Pain-Pleasure.* The writer has been accustomed for several years to call especial attention of his psychology students to a peculiar analogy between the conditions of pleasure and pain in the bodily sphere and the psychical pleasures and pains. It is easily seen that the purely physical pains have the common character of involving a disproportionateness of stimulus to the conveying power of the organ. In other words summation is a dominant neural note in pain. The apparent exceptions are not really so. Thus the observed fact that a depressed nervous state is conducive to painful impressions (as is also fatigue) is but the opposite way of creating the disproportion between stimulus and conveying (or receiving) power from that of rapidly augmenting the stimulus. Central states which impair the viability of tracts have the same effect. Monotony is a mode under fatigue. In all the recent discussions of pain nerves and painful sensations one very obvious consideration is strangely overlooked. It is this: in the majority of cases the interval noticed to intervene between the tactile and the painful sensation is the measure of the time necessary for certain vascular changes to occur. The close relation between pain and vascular change has often been noted. The writer has given special illustrations of this relation in the *Psychological Review*. Now it is easy to trace the connection between the after-pain of a blow (on the toe for example) and the ensuing nervous congestion. It will be found that in less conspicuous instances the same is true. Even in burns, where the slow conduction of heat in the skin is often ignored, there is the after pain due to the vascular change following. The congestion of local capillaries is a condition especially adapted to produce summation, just as the later stages of repair are productive of irradiation. It is not necessary to seek special pain nerves if the clue here pointed out be followed up. The slowness of the pain current, as so often noted, is seen to rest in the prerequisites of summation processes. On the other hand the simplest form of pleasure—that of tickling or the satisfaction growing out of tactile contact—rests upon irradiation. The anatomical basis for peripheral (as contrasted to central) irradia-



tion has been clearly made out by Dogiel in the anastomoses between the tactile corpuscles. It is a remarkable confirmation of the theory that pleasures of the tactile sphere are based on irradiations that, in the case of the most intense pleasure, the skin is most thoroughly and elaborately provided with the anastomosing fibers for irradiation. See his article on the nerves of the skin of the sexual organs. Of course, in the case of the central connections there is always opportunity for more or less irradiation. Association tracts in the cortex are special cases of provision for irradiation or, at least, the application of that principle of nervous overflow. It is not difficult to trace a useful analogy between the pleasures of the higher cognitive faculty and the irradiation in the skin. In both cases the central condition is also important. If the system is keyed up, much greater irradiation is possible (as is very plain in tickling or the erotic excitement). It is not our purpose to carry this thought into its logical conclusion in the higher sphere, though it follows naturally enough from the above that a close similarity can be traced into the emotional field.

The theory above indicated was first outlined in this journal (Vol. V, p. 1) but in several respects the statement suffered from insufficient recognition of the contrast between the summation and irradiation processes, though their close relation was fully recognized.

*The Dynamic Character of Consciousness.* All the results of our recent studies serve but to enforce the truth that all conscious acts are dynamic. There is no such thing as a state of consciousness. The old idea that a sensory stimulus terminating in a receptive cell sets up a change in its condition which is in itself the physical basis of a simple conscious state—a sensation, for example—finds no confirmation in the structure of the organ. In every case apparently there is a reflux wave. Thus it may be believed that all the earlier receptive currents set up responsive overflowing currents. In the case of stimuli which are not capable of localization, the pleasure-pain element which is bound up with everything entering consciousness is not otherwise employed; but in the case of peripheral stimuli these same

factors are used in the manufacture of local signs and cease to have the direct impulsive power. The type of nervous activity being the reflex circuit, the arcs lying within the conscious sphere retain their impulsive nature in one form or another. The modern investigations which seem to identify a motor element in emotion, as well as back of will, enforce the truth that the dynamic element is attached to the stimuli of all conscious states so that it is not necessary to search for some special energizing power in the nature of will. In a recent paper by Professor A. T. Ormund noticed elsewhere in this number this fact is clearly recognized. He says: "What we call will can, in these early psychical activities, be nothing but the conscious responses by which the organism effects its assimilative and adaptive movements." It is then only what we should expect when all kinds of presentation to consciousness prove dynamic and these impulses only need to be illuminated by intelligence to form elementary acts of will. When choice enters, inhibition is the added element. The fact that the resultant (act) is evidently not an algebraic sum of the external stimuli but a product of the internal (vestigial, etc.) conditions into the former gives us the intuition of freedom. Ormund goes further and claims that in all judgment the central thing is a volitional impulse. Thus "the judgment puts a kind of personal stamp of endorsement on the object of perception."

## INQUIRIES REGARDING CURRENT TENDENCIES IN NEUROLOGICAL NOMENCLATURE.

By C. L. and C. JUDSON HERRICK.

In the course of the preparation of the neurological articles for the proposed Baldwin DICTIONARY OF PHILOSOPHY AND PSYCHOLOGY the vexed question of nomenclature was one of the first to be encountered. The great diversity in the usage of different authors, and, indeed, of the same authors at different times in some cases, and, in particular, the recent rapid development of entirely new lines of research involving the introduction of new terms, make it a matter of no small difficulty to determine what is the actual current usage. The most direct way to approach this fundamental matter seemed to us to be that of the questionnaire. We have, accordingly, framed a few questions and circulated them among some of the leading neurologists. It was not our purpose to draw up an exhaustive list of debatable terms. Such lists have been published by the German Nomenclature Commission (*Archiv f. Anatomie und Physiologie*, 1895), by Dr. Wilder (*Jour. of Comp. Neurology*, Dec., 1896) and by others. Our aim was, rather, to select terms which would be representative of their kind and which would reveal the tendencies of the current neuronymic movement in this country and abroad. These circulars were mailed to about 150 of the leading neurologists and anatomists of the world, selected, so far as possible, impartially on the basis of their eminence as investigators or teachers (62 American and 84 Foreign). Replies were received from about one third of those addressed (27 American and 19 Foreign), and the answers, though fewer in number than we had hoped, may, we think, be regarded as fairly representative of the most eminent neurological ability of the United States and Canada, England, and Germany, with a few names from other countries.

In view of the expressed purpose of the German Nomenclature Commission to re-open the discussion of the question of anatomical nomenclature next year, it seems desirable to publish, with the consent of Professor Baldwin, at this time a summary of the results of the questionnaire; we therefore give below the text of the circular with an annotated statement of the replies, the paragraphs of the statement being numbered to correspond with those of the circular.

DEAR SIR :

In connection with the preparation of a DICTIONARY OF PHILOSOPHY AND PSYCHOLOGY, to be issued in London and New York by the Macmillan Co., under the editorial charge of Prof. J. Mark Baldwin, it is desired to determine both the current and the preferred usage in the case of a number of neurological and anatomical terms. We beg, therefore, to request that, in the interests of greater consistency and uniformity of terminology, you will respond as early as possible to the questions below and return the answers to C. L. HERRICK, SOCORRO, NEW MEXICO, U. S. A. We should be glad for permission to cite your opinion; but if, for any reason, you desire not to be quoted and so indicate, the answers will be compiled without reference to the source. In either case please add your signature to the blank.

1. What do you consider the prevailing and preferred usage (the latter in parenthesis and underscored) for terms of anatomical position and direction, e. g. :

- (a) Toward the cephalic extremity of the body axis.....
- (b) " " caudal " " " " .....
- (c) " " dorsal aspect of the body.....
- (d) " " ventral " " " " .....
- (e) " " periphery of a limb or member.....
- (f) " " central end " " " " .....

2. Are the terms "forward," "backward," "above," "below," "descending," "ascending," "higher" and "lower" (or their German, French, etc., equivalents) ambiguous as applied to directions and positions in the central nervous system; and, if so, how may the ambiguity best be avoided? .....

3. Do you favor the reduction of polynomial descriptive terms to mononyms so far as possible, as

(a) By dropping the substantive in such terms as (corpus) callosum and (area) opaca? .....

(b) By substituting compound mononyms for polynomial expressions, as "medipedunculus" for "brachium pontis cerebelli" or "preperforata" for "area perforata anterior"? .....



4. Kindly underscore your preference among the following, making any comments or additions which may seem best to you :

- (a) *Proton, fundament, rudiment* for the German *Anlage* ;
- (b) *neurocyte, neurodendrite, neuron, nerve cell, ganglion cell* for the nerve unit ;
- (c) *gangliocyte, aesthesioblast, ganglion cell* for cells of peripheral ganglia ;
- (d) *nidulus, nidus, nucleus* for central cell cluster ;
- (e) *rhombencephalon* (=myelencephalon + metencephalon, His), *myelencephalon, metencephalon* as segmental term for hind-brain ;
- (f) *iter, aquaeductus Sylvii, mesocoele* for cavity of mesencephalon ;
- (g) *metacoele, ventriculus quartus* for the fourth ventricle ;
- (h) *epiphysis, glandula pinealis, conarium, corpus pineale* ;
- (i) *hypophysis, pituitary (body)* ;
- (j) *neuron, neuraxis, myelencephalon* for axis cerebro-spinalis.

5. Should "fissura" and "gyrus" be limited to the cerebrum and "sulcus" and "folium" to the cerebellum ?

Very respectfully,

C. L. HERRICK.

Socorro, New Mexico, December, 1896.

In the following statement the number following a given term indicates the number of authors who favor the use of that term. To facilitate the comparison of the American with the European authors, the number of authors of each class is added, *Am.* signifying replies from the United States and Canada, *Eu.* signifying replies from Europeans (including one from New Zealand).

# 1. Terms of position and direction.

- (a) cephalad, 20, Am., 18, Eu., 2.
- cephalic, 3, Am., 2, Eu., 1.
- cephalically ?, 1, Eu., 1.
- cranial (cranialis), 4, Eu., 4.
- frontal, 3, Eu., 3.
- anterior(ly), 4, Am., 3, Eu., 1.
- rostrad, 2, Am., 1, Eu., 1.
- rostral, 1, Eu., 1.
- upward, 2, Am., 1, Eu., 1.
- apical, 1, Eu., 1.
- capital, 1, Eu., 1.
- toward the head, 1, Eu., 1.

Pread and postad are given as alternatives to cephalad and caudad by two American authors. The three who favor cephalic apparently would not admit cephalad.

- (b) caudad, 23, Am., 19, Eu., 4.  
caudal, 13, Am., 3, Eu., 10.  
caudally, 1, Eu., 1.  
posterior(ly), 6, Am., 4, Eu., 2.  
downward, 2, Am., 1, Eu., 1.  
terminal, 1, Eu., 1.
- (c) dorsad, 22, Am., 19, Eu., 3.  
dorsal(ly), 22, Am., 8, Eu., 14.  
dorsal to, 1, Eu., 1.  
back, 1, Eu., 1.
- (d) ventrad, 22, Am., 19, Eu., 3.  
ventral(ly), 22, Am., 8, Eu., 14.  
ventral to, 1, Eu., 1.  
front, 1, Eu., 1.
- (e) peripheral(ly), distal(ly), 32, Am., 15, Eu., 17.  
peripherad, distad, 14, Am., 12, Eu., 2.

A confusion arose between distal end and periphery, but the intention evidently was to use the terms consistently in each case.

- (f) proximal(ly), 23, Am., 9, Eu., 14.  
proximad, 11, Am., 9, Eu., 2.  
central(ly), 9, Am., 6, Eu., 3.  
centrad, 3, Am., 3.

## 2. Are vernacular terms ambiguous?

- yes, 24, Am., 16, Eu., 8.
- no, 15, Am., 6, Eu., 9.

Several of the authors who deny the ambiguity of these terms do so with the qualification that they are not ambiguous if applied alike to all animals; but inasmuch as some of them would apply the terms to the human body prone, while others insist that they must be "referred to the human body in the erect position," we find in fact that the ambiguity re-appears in the very statement that there is no ambiguity. Of those who recognize the ambiguity, most would avoid it by the use of an intrinsic terminology, others frankly give up the attempt to avoid it except by the context. The intrinsic terms, cephalic, cranial, caudal etc., are almost universally adopted as the preferred terms. The compounds in -ad are not so generally ad-

mitted, and in several cases in which they are adopted on account of their great practical utility it is with the reservation that they will be called for only very sparingly.

### 3. Reduction of polyonyms to mononyms.

- (a) by dropping substantive.  
yes, 21, Am., 18, Eu., 3.  
no, 21, Am., 7, Eu., 14.
- (b) by compounding.  
yes, 17, Am., 15, Eu., 2.  
no, 24, Am., 9, Eu., 15.

A large proportion of those favoring the reduction to mononyms qualify it by stating that ambiguity must be avoided, the compound terms must be etymologically correct, etc.

- 4. (a) proton, 13, Am., 7, Eu., 6.  
Anlage, 11, Am., 8, Eu., 3.  
rudiment, 9, Am., 5, Eu., 4.  
fundament, 6, Am., 3, Eu., 3.  
foundation, 1, Am., 1.  
origin, 1, Am., 1.  
beginning, 1, Am., 1.

The term rudiment was in several cases recommended as opposed to vestige, thus removing any possible ambiguity. It is probable that this is the consensus of opinion of those who recommend this term.

- (b) neuron, 27, Am., 12, Eu., 15.  
neurone, 1, Am., 1.  
neure, 1, Am., 1.  
neurocyte, 8, Am., 7, Eu., 1.  
nerve cell, 8, Am., 5, Eu., 3.
- (c) ganglion cell, 23, Am., 9, Eu., 14.  
gangliocyte, 8, Am., 5, Eu., 3.  
aesthesioblast, 1, Am., 1.  
sensi-neuron, 1, Am., 1.  
sensory neuron, 1, Am., 1.  
nerve cell, 1, Eu., 1.
- (d) nucleus, 25, Am., 12, Eu., 13.  
nidus, 10, Am., 8, Eu., 2.  
nidulus, 1, Eu., 1.  
neuronidulus, 1, Am., 1.  
cell group; 2, Am., 2. recommended as an alternative with nucleus.

This last usage has much to commend it. The compilers of this report, feeling that the double ambiguity of *nidus* is absolutely fatal to its application in this connection and recognizing that none of the other terms proposed have met with general acceptance, are constrained to recommend the continued use of *nucleus* when a Latin term is necessary.

- (e) metencephalon, 16, Am., 9, Eu., 7.
- rhombencephalon [His], 13, Am., 6, Eu., 7.
- myelencephalon, 4, Am., 3, Eu., 1.
- hind brain (cereb. + medulla), 1, Am., 1.

The confusion prevailing here is largely a morphological one. The term metencephalon in some cases expressly excluded the cerebellum, in others it was left ambiguous; this term was used twice in addition to those above, where it was expressly applied to the cerebellum alone.

- (f) aquaeductus Sylvii, 18, Am., 4, Eu., 14.
- mesocoele, 13, Am., 10, Eu., 3.
- iter, 11, Am., 11.
- mesocoele = iter + optocoeles, 1, Eu., 1.
- (g) ventriculus quartus, fourth ventricle, 24, Am., 11, Eu. 13.
- metacoele, 16, Am. 12, Eu., 4.
- rhombocoele, 1, Am., 1.
- (h) epiphysis, 36, Am., 23, Eu., 13.
- corpus pineale, 3, Eu., 3.
- glandula pinealis, 3, Eu., 3.
- conarium, 1, Am., 1.

Besides the above, one American writer uses epiphysis for the outgrowth connected with the brain, pinealis and paraphysis for those which become separated.

- (i) hypophysis, 39, Am., 23, Eu., 16.
- pituitary body, 5, Am., 2, Eu. 3.
- (j) neuraxis, 12, Am., 8, Eu., 4.
- myelencephalon, 11, Am., 6, Eu., 5.
- cerebro-spinal axis, 7, Am., 3, Eu., 4.
- neuron, 5, Am., 4, Eu., 1.
- central nervous system, 1, Am., 1.
- 5. yes, 11, Am., 8, Eu., 3.
- no, 21, Am., 9, Eu., 12.

It is obvious that our hope of being able to deduce from these replies a standard or norm of current nomenclature has



been vain. The diversity is the only thing which stands out prominently. Nevertheless in this country the results of persistent agitation and particularly of the uniform recommendations of the several anatomical and medical societies are clearly manifest. The danger of "the formation of a peculiar anatomical vocabulary in America," such as seriously to impede scientific intercourse with other countries does not, however, seem to be imminent. There is a tendency, often implied and sometimes clearly expressed, to return to the simplest English words which can be found adequate to express the meaning.

On many points, such as the dropping of certain substantives, the authorities are so evenly divided that each must form his independent judgment. Such points are not matters of vital importance, as all will admit, and may properly be left, like most other questions of nomenclature for that matter, with the working neurologists, among whom they will in time come to a condition of stable equilibrium. The unification of our nomenclature is to be accomplished, if at all, by a process of survival of the fittest among competing terms at the hands of our working anatomists rather than by legislative enactment. Yet the international discussions now in progress may do much to further this end.

A CONTRIBUTION ON THE MOTOR NERVE-ENDINGS  
AND ON THE NERVE-ENDINGS IN THE  
MUSCLE-SPINDLES.

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By far the greater number of all the communications dealing with the ending of nerves in muscle tissues pertain to observations made on muscle tissue impregnated with one or the other of the several gold chloride methods; valuable as such observations have been, they yet leave many of the details more or less unsatisfactorily answered. Since the introduction of the chrome-silver and methylene blue methods, some further facts, tending to clear up some disputed points, have been gathered.

At the outstart however—and without in the least attempting to throw discredit on the many important observations which have been made with the Golgi method, greatly furthering our knowledge of the structure of the central and peripheral nervous system—it may be stated that so far as pertains to the relation of the ultimate endings of the nerve fibers to the structural elements of the several motor tissues, the Golgi method does not seem so applicable as its rival, the methylene blue method. The great advantage which this latter method has over both the gold chloride and the chrome-silver methods lies in the fact that in the most *successfully stained* methylene blue preparations, only the nerve fibers and their ultimate endings are colored, while the other tissues remain practically unstained. The observations on the endings of nerves in motor tissues made with the methylene blue method have revealed

most clearly the shape and arrangement of the ultimate branches of the axis cylinder; there exist however differences of opinion as to the relation of such endings to the muscle fiber or muscle cell, its sarcolemma, muscle substance and muscle nuclei. This, we believe, is largely due to the fact that such observations have been made on methylene blue stained tissues fixed in ammonium picrate and cleared in glycerine. Tissues prepared by this method are usually examined in relatively large pieces or in teased preparations and, while many important observations may be made on such preparations, as the results of Dogiel and Retzius may show, the observer is often left in doubt concerning this or that point of interest.

It occurred to us that by using the *intra vitam* methylene blue method of Ehrlich as improved by Bethe, where the stained tissues are fixed in ammonium molybdate, and may then be embedded in paraffin, sectioned and double stained, it would be possible to obtain surface views, longitudinal and cross sections of the motor endings in relatively thin sections, so stained that the nerve and its terminal apparatus would be blue and all other structures red. Such preparations, we hoped, would throw new light on some of the disputed points and confirm facts more or less clearly established. We trust the facts to be presented may substantiate our expectations.

It was our wish to make the investigation more comprehensive, especially that portion which pertains to the motor endings in striped muscle and heart muscle, but other duties have interfered. It is thought however that enough observations are at hand to admit of drawing some general conclusions, and further, that this exposition of the results obtained with this method, may stimulate others to its use in similar investigations.

The material was obtained as follows :

*Motor endings :*

- a. striped muscle, rabbit and frog (*Rana halecina*);
- b. heart muscle, cat ;
- c. involuntary muscle, cat, tortoise (*Chelydra serpentina*), and frog (*Rana halecina*).

*Nerve ending in muscle spindle :*Amphibia, frog (*Rana halecina*);Reptilia, tortoise (*Chrysemys picta* and *Emys melagris*);

Bird, dove;

Mammalia, dog, cat, rabbit, Guinea pig and rat.

*Method:* The methylene blue method has alone been used. A 1% solution of methylene blue in normal salt was injected either into the living animal, or (in staining the nerves in muscle spindles, the intrinsic plantar muscles being used almost exclusively) into the abdominal aorta after bleeding the animal. From 45 minutes to an hour after the injection, the tissues to be studied were removed to a slide moistened with normal salt solution, where they remained until the blue color was developed in the nerve fibers, this being controlled under the microscope. As soon as the nerve endings seemed well stained, some of the pieces of muscle were placed in the following fixative:

Ammonium Molybdate.....	1 gm.
Aqua Dist. ....	10 c. cm.
Hydrochloric Acid.....	1 gtt.

This fixative, which is only very slightly modified from that suggested by Bethe, needs to be cooled to nearly zero, before placing the tissues into it; it is therefore well to prepare it before the injection is made, and to surround it with ice, so that it may be properly cooled before using. In this fixative, the tissues remain from 6 to 12 hours; they are then washed in distilled water and hardened in absolute alcohol; embedded in paraffin and cut in serial sections. The sections were fixed to slides with albumen fixative and counter stained in alum carmine or alum cochineal and mounted in balsam. Others of the muscle pieces, especially those stained for the nerve ending in spindles, were fixed in a saturated aqueous solution of ammonium picrate (Dogiel); cleared in equal parts of ammonium picrate and glycerine and teased under the dissecting microscope, and mounted in the picrate-glycerine mixture. In this way, it was often possible to obtain very complex nerve end-



ings, with the nerve fibers going to them, as some of our figures may show. The capsules of the spindles are in this way not shown and the intra-fusal fibers only faintly seen.

*Motor endings in striped muscle.* It is not our purpose to give a full review of the literature bearing on the motor endings in striped muscle tissue. This has been so well done in the writings of Krause, Kühne and Ranvier that such a summary is here uncalled for. Mention may however be made of the fact that Doyère, as early as 1840, discussed the endings of nerves in striped muscle of insects; describing a granular expansion of the nerve which seemed to be glued to the muscle substance, and which was found under the sarcolemma; the term "*Doyère's elevation*" comes from this account. Kühne discovered in 1862 the branched ending of the axis-cylinder in frog's muscle. In the same year, Rouget described an end-plate, which was said to be under the sarcolemma. This was regarded as the expanded end of the nerve fiber, its nuclei similar to the nuclei found in the nerve sheath. Rouget's observations were made on reptilia, birds and mammals. Further advance was soon made by Krause, who observed that the axis cylinder did not form the end-plate by its expansion, but terminated in a number of pale fibers, in a fibrillar, nucleated capsule, which was regarded as an expansion of the nerve sheath and which was outside of the sarcolemma. A much more accurate account, as we now know, was given by Kühne in 1864, where, especially in his later communication, he states that the nerve ending is under the sarcolemma, the nerve sheath becoming continuous with the muscle sheath. And further states that the myelin stops abruptly, while the axis cylinder divides into a number of branches, which terminate in an elevation on the muscle fiber. In his classical research, which appeared in 1887, Kühne says that at the point of innervation of a striped muscle fiber, the following structures are to be recognized:

1. The telolemma with its granular nuclei.
2. The branches of the axis cylinder—" *Das Geweih*."
3. The sole (" *Die Sohle*"), consisting of a granulosa with large transparent nuclei.

Consequent on the results obtained with the methylene blue method in staining other nerve end-organs, this method was also employed to stain the nerve ending in striped muscle tissue, and there now exist a number of communications, giving results obtained with this method, of which observations, those of Arnstein, Cuccati, Gerlach, Feist, Dogiel and Retzius will be considered.

In discussing our own observations, those made on the rabbit will first be considered. Here, as in many other vertebrates (Reptilia, Birds and Mammals), a localized ending, a motorial end-plate, is found, presenting a more or less distinct elevation at the point of entrance of the nerve fiber.

The relation of the "motorial end-plate" or the "motor ending" to the muscle fiber may first be discussed. The great majority of all the observers are in accord in regarding the motor end-plate as under the sarcolemma, although some few observers still describe it as outside of the sarcolemma; Kölliker, closing his remarks touching this point, says, "das sowohl eine hypolemmale als eine epilemmale Lage derselben (motorial end-plate), ihre Vertheidiger hat;" while Böhm and Davidoff refer to it as "der am meisten bestrittene Punkt;" and Krause regards the end-plate as the continuation of Henle's sheath, which surrounds the entire end-organ and unites it to the sarcolemma.

Cross sections are of course most suitable for answering this question. No doubt the difficulty experienced by Kühne and van Syckle in making cross sections of motor endings stained in gold chloride has deterred many from further pursuance of this procedure, and yet the results obtained by them, if one may judge from Kühne's account and figures (Fig. 30 to 40, Plate B.) show most clearly that the end-plate is under the sarcolemma, as does also Fig. 79 of Böhm and Davidoff's textbook.

In Fig. 6, 7 and 8, are shown three longitudinal sections and in Fig. 9, 10 and 11, three cross sections of motor endings taken from longitudinal and cross sections of rabbit's muscle, the nerves of which had been stained in methylene blue,

the sections, about 20  $\mu$  in thickness having been counter stained in alum carmine.

A study of these figures will show that, in case the sarcolemma (*S*) is clearly made out, it passes over the motorial end-plate. The sections from which these figures were taken, as also many others, leave no doubt concerning this point.

Most writers have agreed with Kühne in stating that the neurolemma of the nerve fiber terminating in the end-plate is continuous with the sarcolemma, covering the end-plate. This we can confirm in our sections, as Fig. 4, 7, 10 and 11 may show. In these figures, *n. l.*, the neurolemma can be traced with the utmost clearness into *S*, the sarcolemma.

*The termination of the axis-cylinder—das Geweih.* Writers are agreed that the arborescent figure seen in the motorial end-plate when stained with the various dyes, is the continuation of the axis cylinder of the medullated fiber terminating in the motor ending. This is most clearly seen in a striped muscle, the motor endings in which have been stained *intra vitam* with methylene blue. In well stained preparations, only the axis cylinders and their branched endings are stained blue, all other structures remaining unstained. The branched endings of the axis cylinder in a motorial end-plate may thus be regarded as the end-brush, or more correctly speaking, one of several end-brushes, of the neuraxis of a motor neuron.

Kühne has most carefully studied the structure of these branched endings of the axis cylinder—*das Geweih*—in gold chloride preparations, and, without going into a lengthy account of the results obtained by him, the following brief statement may be given to show his conclusions as to their structure. Kühne describes an axial fiber as axial tree—*Axialbaum*—which stains more deeply in gold chloride and is looked upon as representing the ultimate fibrillæ of the axis cylinder, and a *stroma*, which in the living axis cylinder and end-branches is distributed between the ultimate fibrillæ, but in the gold chloride preparations, forms a peripheral zone, surrounding the axial fibers; this does not stain in the gold solutions or stains only very lightly. This differentiation is well shown in Kühne's figures

of the cross sections of the motor endings (Fig. 30 to 40, plate B).

The structure of the end-branches of the axis cylinder in motor endings has further been discussed by Feist, Cuccati and Retzius, based on observations made with methylene blue, and while they consider more particularly the motor endings in amphibian muscle, their results may here be presented. Feist is entirely in accord with Kühne's views. He states that, in methylene blue preparations of frog's muscle, further stained in picro-carmin, the axial thread retains the blue color while, in the stroma, the blue is either entirely displaced by the picro-carmin or it collects in irregular granules. Cuccati describes blue granules in the peripheral part of the branches of the axis cylinders ending in the striped muscle of frog and triton, when stained in methylene blue and fixed in ammonium picrate, and Retzius finds both axial threads as described by Kühne and Feist and the peripheral granules (*Randkörner*) described by Cuccati in frog's muscle similarly treated.

Retzius states however—a point which we will emphasize—in discussing the nerve ending in frog's muscle, that even with very high magnification (Winkel's Imm. Obj. 1-24 and Ocul. 3) "konnte ich keine Structur in den durch Methylenblau gefärbten Endscheiben wahrnehmen. Erst nach dem Zusatz von pikrinsauren Ammoniak trat die üblich 'Differenzierung' hervor." We may finally add the following comment made by Schäfer on Kühne's observations as above given: "Kühne regards the axial part as representing the fibrils of the axis cylinder, but it may be doubted whether the differentiation into axial part and stroma is not due to the shrinking of the axis cylinder under the influence of the reagent."

Our own observations on this point are as follows: In striped muscle tissue from the rabbit, stained *intra vitam* in methylene blue, removed to a slide and examined at once, (1-12 oil imm. and No. 3 ocul. Leitz), no structure whatever can be made out in the arborescent nerve ending. All the branches of the axis cylinder have a homogeneous blue color, and while they often show slight thickenings and here and there



short side branches, they are nevertheless of a very regular contour. If the same preparation is set aside for a short time, 10 to 15 minutes, and is again exposed to the air by the removal of the cover glass, and then again examined, small blue granules and now then an axial thread may be seen in many of the end-branches of the axis cylinder.

In tissues fixed in ammonium molybdate, sectioned and double stained in alum carmine, the branches of the axis cylinder present different appearances. In some motor endings, Fig. 3, a distinct axial thread and stroma may be made out; this is, however, only rarely seen. More often the branches of the axis cylinder present a fine granular appearance; irregular granules varying in size and the intensity with which they are stained, and distributed, sometimes evenly through the end-branches, or again only in their peripheral portion, may be seen. Fig. 4 to 8 show this. It may in fact be stated that the end-brush of a motor nerve, meaning by that the branched ending of an axis cylinder in a motorial end-plate, is structurally very similar to the nerve fibers and their branches in other nerve endings when stained in methylene blue and fixed in ammonium molybdate. We are therefore led to conclude, basing this statement on a somewhat extended experience with the *intra vitam* methylene blue method, that the differentiation which has been observed and described, in the structure of the end-brush of a nerve fiber ending in the motorial end-plate, depends, to some extent at least, on the method used to stain it; and, if the methylene blue method is used, on the time intervening between their successful staining and their fixation, and also on the fixative used. In this connection, it may further be said that a comparison of the figures given by observers using the methylene blue method in staining the motor endings with those current in our text books and with Kühne's excellent and numerous figures will show that the branches of the axis cylinder appear much smaller in methylene blue preparations than in those stained with gold chloride; the former method, it would seem, portrays much more nearly the actual conditions. This at least seems to be the case when such motor endings are com-

pared with nerve endings in other tissues. Thus far in our discussion, no mention has been made of the behavior of the myelin of the medullated fiber ending in the motorial end-plate. This, as is well known, stops abruptly as soon as the sarcolemma is reached by the nerve fiber; this fact is confirmed in our preparations, the myelin often staining faintly blue.

Before leaving the discussion of the ending of the axis cylinder in the motorial end-plate, attention needs to be drawn to some curious endings now and then seen among the endings thus far described. One such is shown in Fig. 2. As may here be seen, the axis cylinder terminates in an ending which does not in the least resemble the ones shown in the other figures. Instead of fine branches which may clearly be made out, we have here short, coarse and very granular fibers which seem to anastomose. We are thus far unable to give any explanation of these structures, the more so since they have been met only a few times, but always in muscle in which the great majority of the motor endings seemed in every way normal. They are mentioned here simply as a curious anomaly.

*The sole and its nuclei.* The granular mass, in which the nerve fiber terminates, was at first looked upon as the expanded end of the nerve fiber—Doyère, Engelmann and also Kühne in his earlier writings. Kühne deserves the credit of the discovery that the axis cylinder terminates under the sarcolemma in the nucleated granular substance which he described as the sole (*Sohle*); the nuclei, as sole nuclei (*Sohlenkerne*).

This granular sole differs greatly in its behavior toward staining reagents, even in its reaction to the same stain in different parts of the same preparation. In some of the gold chloride preparations, it remains entirely unstained, in others, is only faintly stained, and in still others, it takes a reddish color somewhat deeper than the muscle substance yet less deep than the branches of the axis cylinder; usually the nuclei of the sole may be made out more or less clearly. Kühne, and it seems to me very correctly, makes the following comment on this point: "Ohne Zweifel sind in der Deutung der Gold-bilder die gefährlichsten Irrthümer dadurch entstanden dass man die

genannten Inhaltbestandtheile des Nervenbügels nicht genügend unterschieden hat, indem man sich vor allem die Möglichkeit nicht klar gemacht hat, dass die dem Geweih wie ein Teig anklebende Granulosa diesem zugehörig erscheinen muss, wenn sie durch die Färbung nicht genügend davon unterschieden ist." In motor endings stained in methylene blue and examined at once, or fixed in ammonium molybdate and studied in sections, no trace of a granular sole is seen. Both Retzius (for rabbit) and Dogiel (for reptilia) state that in unfixed muscle (stained in methylene blue) the granular sole and its nuclei are not seen. It may however, as they have shown, be brought out with picro-carmin. Opinions still differ as to the nature of the sole. Böhm and Davidoff state that "The substance of the sole may be regarded as an accumulation of neuroplasma, its nuclei corresponding, very probably, to the nuclei of the sarcolemma and those of the neurolemma."

Kölliker, whom we will quote in his own words, has this to say concerning the fine granular substance of the sole. "Entweder entsteht dieselbe durch eine Wucherung der Zellen der Schwann'schen Scheide, die auch bei den Endplatten die Endäste oder Achsencylinder bekleiden und würde sich so erklären, dass diese granulirte Substanz Kerne enthält, die nicht an den Endfasern direkt ansitzen. Oder es ist dieselbe sammt den eben erwähnten Kernen eine Fortsetzung der Hensle'schen Nervenscheide, welche wie Krause annimmt, die gesammte Endplatte umhüllt und mit dem Sarcolemma verbindet, eine Aufstellung, die eine epilemmale Lage der Rouget'schen Endplatten voraussetzen würde."

In his later writings, Kühne, if we understand him correctly (pages 91-92), suggests the hypothesis that the granular sole might be looked upon as muscle protoplasm—sarcoglia or sarcoplasm, while the nuclei of the sole might be likened to muscle nuclei. This interpretation of the granular sole and its nuclei suggested itself to us before Kühne's similar observation was definitely understood.

In all our sections of striped muscle of the rabbit, in which the motor endings were well stained in methylene blue and in

which the sections were further stained in alum carmine, nothing is seen of a granular sole; as, for instance, Figs. 1, 3, 4 and 5 may serve to show. In longitudinal or cross sections of the motor endings in rabbit's muscle (stained as above indicated) what has been described as a granular sole may be observed as a nearly homogeneous substance, continuous with the sarcoplasma found between the muscle fibrillæ and staining in every way like it, as may be seen in Fig. 6 to 11.

Such observations have led to the conclusion that what has been described as the granular sole may be regarded as an accumulation of sarcoplasma continuous with the sarcoplasma of the muscle. The nuclei of the sole are in structure very similar to the muscle nuclei, and we have regarded them as such. As our figures may serve to show, especially those showing a longitudinal or cross section of the motorial end-plate, the branches of the axis cylinder—the end-brush of the neuraxis of a motor neuron—terminate in this mass of sarcoplasma, the muscle nuclei, which are here found in relatively large numbers, being both above and below the terminal branches of the axis cylinder. Schäfer states that “applied to the branches of the ramifications, small granular nuclei are seen at intervals; these nuclei of the arborization are different from the clear nuclei of the bed and also from the flattened nuclei of the sheath, which lie directly under the sarcolemma covering the end-plate, and which resemble the nuclei of the sheath of Schwann covering the nerve.” Nuclei applied to the branches of the axis cylinder have also been described by Ranvier and Kölliker, while Kühne does not recognize them. In none of our preparations made from rabbit's muscle were such nuclei (*Gerweih-kerne*) seen. In our sections, nuclei which seemed in very close apposition to some one of the terminal branches, were now and then seen. Such nuclei had not, however, a distinctive structure.

The telolemma nuclei described by Kuhne and others, were now and then recognized in our sections. They are more oblong and stain more deeply than the muscle nuclei. See *t*, *n*, of Figs. 3, 4, 5, 7, 9 and 11.



*The motor ending in striped muscle of amphibia.* As is well known, in amphibia the axis cylinder of the motor fibres terminating in striped muscle does not end in a localized area (birds, reptilia and mammalia), but ramifies over a proportionately much larger area, forming the so-called "*Stangen-geweih*," as was first correctly pointed out by Kühne. The form of this ending is so well known that a further description seems superfluous. There is, however, one point, concerning which investigators are still not agreed; namely, the relation of the end-branches of the axis cylinder to the sarcolemma of the muscle fibers. We trust our observations may be of some value in settling this point.

Following Kühne, many observers have stated that the ramifications of the axis cylinder of the motor nerves terminating in striped muscle of amphibia are under the sarcolemma, while Krause, Kölliker, Sihler and, to some extent, also Retzius contend that these endings are wholly or in part outside the sarcolemma.

Kölliker has this to say concerning these endings: "Die Nervenfasern gehen zuletzt in blasse Endfasern über, die alle aus einer Fortsetzung der *Schwann'schen* Scheide und des Achsencylinders bestehen und da und dort dieselben Kerne zeigen, die auch in der Schwann'schen Scheide der noch dunkelrandigen angrenzenden Nerven sich finden." "In Betreff der Lage dieser Endäste stehen sich immer noch zwei Ansichten gegenüber, indem die Einen mit Kühne dieselben zwischen das Sarcolemma und die Substanz des Muskelfaser verlegen, die anderen mit mir und Krause der Meinung sind dass dieselben auf dem Sarcolemma ihre Lage habe."

Sihler, in two publications giving the results of observations made with two methods which he himself has devised (see his accounts for these methods), expresses himself very strongly in favor of an epilemmal ending of the nerve fibers in frog's muscle.

The conclusions expressed in his earlier communication may serve to show his position. "The whole nerve ending is situated on the outside of the sarcolemma, and, like the capil-

laries, embedded in the gelatinous connective tissue." This opinion is very largely confirmed in his second paper.

In the account given by Retzius, who has worked on the motor nerve endings in frog's muscle with methylene blue the following statement may be found: "An den Methylenblaupräparaten konnte ich ferner nie sicher sehen, ob die Endplatten auf oder unter dem Sarcolemma liegen, so dass ich zur Lösung dieser alten Streitfrage nichts beitragen kann." And again,—“Die leichte, reine Färbung der Nervenfasern und ihrer Endscheiben, ohne gleichzeitige Färbung des Inhalts der Muskelfaser, scheint mir indessen für eine Anhaftung an der Aussenseite des Sarcolemmas zu sprechen, denn an den abgerissenen Enden der fraglichen Muskelfasern sah ich in der Regel gleichzeitig eine diffuse Bläuung des Muskelfaserinhalts.”

This question, it seemed to us, might be most satisfactorily answered in cross and longitudinal sections of the motor endings in amphibian muscle stained in methylene blue and further treated as designated. Two such cross sections are shown in Figs. 13 and 14. It may here be seen that the ramifications of the axis cylinder are under the sarcolemma terminating in a relatively thin layer of sarcoplasma, which layer of sarcoplasma is continuous with that found between the muscle fibrillæ.

The conditions here presented being therefore very similar to those found in such vertebrates as present a localized motorial ending, with the distinction that in the latter the axis cylinder terminates in a localized elevation—the sole—which has been interpreted as being a circumscribed accumulation of sarcoplasma, while in amphibia the sarcoplasma surrounding the ramified ending of the axis cylinder, extends, like it, over a larger proportionate area of the muscle fibre.

The figures here shown, and many others that might be sketched, would seem to confirm most fully the belief in a hypolemmal ending of the axis cylinder in striped muscle of amphibia. In fresh methylene blue preparations of the motor endings, studied in a thin muscle, as for instance the cutaneous pectoris (Ecker), the axis cylinders of the medullated nerves may be traced with the utmost clearness into the ramifications,

which we believe are under the sarcolemma. The terminal branches which are non-medullated, are entirely devoid of any sheath; even under the 1-12 in. oil imm., no trace of the sheath of Schwann, which, according to Kölliker, accompanies such branches to their termination, can here be made out. The same may be said of muscle stained in methylene-blue and cut parallel to the long axis of the muscle fibers, the sections being further stained in alum carmine. The terminal branches (hypolemmal fibers) are, as Fig. 12 may show, devoid of any covering of their own. The neurolemma becomes continuous with the sarcolemma as soon as the nerve fiber passes under the latter. See Fig. 14, *n. l.* Sihler would, if these observations are correct, be in error when he states that neither the sheath of Schwann nor Henle's sheath is continuous with the sarcolemma.

The myelin of the medullated fiber stops abruptly as soon as the axis cylinder passes under the sarcolemma; this point needs no further discussion.

Concerning the structure of the hypolemmal branches of the axis cylinder in frog's muscle, the statements above made on the hypolemmal nerve branches in rabbit's muscle are equally applicable. Kühne and Feist describe an axial thread and stroma; Cuccati, peripheral granules; and Retzius finds sometimes an axial thread, and again the granules mentioned by Cuccati, in picrate of ammonium fixed methylene blue stained muscle tissue, but not in such tissue examined before such fixation. In our sections of frog's muscle, stained in methylene blue and alum carmine, the appearance most generally seen is shown in Fig. 12. The hypolemmal branches present a fine granular appearance, are often more or less varicose and often show marked differences in thickness in the course of a branch. Now and then what might have been interpreted as an axial thread was seen, this, however, very seldom and only in some of the hypolemmal branches.

In sections giving a surface view of the muscle fibers of the frog, double stained in methylene blue and alum carmine, it may be seen that the muscle nuclei are more numerous in that portion of the muscle fiber receiving the ramified ending

of the motor nerve. Many of these nuclei are found in the thin layer of sarcoplasma in which the axis cylinder branches terminate. These nuclei are comparable to the so-called sole nuclei, which, it will be remembered, were also regarded as nuclei of the sarcoplasma—muscle nuclei.

In our sections, we have recognized the nuclei described by Kölliker, Ranvier and others, which form a part of what has been regarded as the hypolemmal portion of the axis cylinder. The nuclei in question are described by Kölliker as the nuclei of the sheath of Schwann accompanying the ramifications of the axis cylinder. That the terminal branches of the axis cylinder are not invested with a continuation of the sheath of Schwann, we have already tried to show; such nuclei, if present, could not, therefore, be regarded as nuclei of this sheath. In our sections, nuclei are sometimes found very near one or the other of the hypolemmal branches of the axis cylinder, as *a*, and *a'* of Fig. 12, may show. The differential staining used by us, and the use of the micrometer screw of the microscope enable us to state that such nuclei are not a part of the terminal branches, but are always more or less distinctly separated from them. Such nuclei have no doubt been interpreted as nuclei of the hypolemmal branches in gold chloride preparations, where such differentiation is not always possible.

Before closing the discussion of the motor endings in amphibian muscle, attention needs to be drawn to a view expressed by Gerlach, namely, that the nerve fibers terminate in an intramuscular network which pervades the entire muscular substance, which network is in connection with the contractile portion of the sarcolemma contents. That we may state Gerlach's opinion correctly, we give here his own words on the subject: "Es existirt innerhalb des Sarcolemmas ein Axenfasernnetz, welches die contractile Substanz durchzieht, das intravaginale Nervennetz. Bei günstiger Goldeinwirkung, erscheint der ganze Muskelfaden von strichartigen Punkten durchsetzt und zwar haben diese gesprenkelten Stellen ganz dieselbe Farbe, wie die intravaginalen Nerven. Demnach muss in dem contractilen Inhalt des Sarcolemmas eine Substanz



vorhanden sein, welche Goldsalze in derselben Weise reducirt, wie die intravaginalen Nerven. Durch weitere Behandlung der Goldpräparate mit Cyankali gelingt es den sicheren Nachweis zu führen, dass zwischen den intravaginalen Nerven und diesen Sprenkelungen directe Continuitätsbeziehungen existiren." This view is defended by Gerlach in his second communication based on observations made with methylene blue. It would seem to us, from Gerlach's descriptions and figures, that both in his gold chloride and in his methylene blue preparations, he has stained the sarcoplasma, in which, as we believe, the axis cylinder terminates. But the mere fact that, in methylene blue, for instance, certain granules and other substances are tinged blue, is not proof positive that these are of a nervous nature; as it is well known that, under certain circumstances, elements other than nerve fibers are stained in methylene blue, even when the blue is injected into the circulation of a living animal. Red blood cells may be stained blue or show blue granules; connective tissue cells; intracellular cement substance; and now and then most clearly yellow elastic fibers may in this way be stained. In well stained motor endings, before fixing or after fixation in ammonium molybdate, when examined under the 1-12 oil imm., not a trace is seen of Gerlach's "intravaginal network" in methylene blue preparations. Dogiel discusses this point in the following words: "Bei einer gehörig gelungen Tinction normaler Muskelfasern ist nichts derartigen zubemerken."

As our observations pertain exclusively to the ultimate ending of the motor nerves in striped muscle, and, as our preparations were made with that end in view, we do not desire here to touch on the general distribution of the motor fibers in striped muscles, on their branching, etc. For answering these questions surface preparations are far more suitable than sections. Our observations admit, we believe, of our drawing the following conclusions as to the structure of the motor endings in striped muscle in the vertebrates examined, and we would venture to suggest that such conclusions apply equally well to motor endings of such other vertebrates as show a structure similar to those here discussed.

(1) The ramified terminations of the axis-cylinder in the motorial endings of striped muscle are the end-brushes of the neuraxes of motor neurons, and are similar in structure to the end-brushes of other cerebro-spinal fibers.

(2) This end-brush (*das Geweih*, Kühne) terminates in the sarcoplasma, therefore under the sarcolemma of the muscle fibers. At the place of ending of the nerve fibers, the sarcoplasma may be accumulated in a circumscribed mass, forming an elevation, more or less distinct, on the side of the muscle fiber, as in reptilia, birds and mammalia, or spread out over a proportionately greater area of the muscle fiber, as in amphibia. In the mass of sarcoplasma, the muscle nuclei (sole nuclei of other writers) are relatively more numerous than in other parts of the muscle fiber.

(3) The neurolemma of the nerve fiber terminating in the motorial ending becomes continuous with the sarcolemma at the point of entrance of the said nerve fiber into the sarcoplasma. Over the endings, sarcolemma or neurolemma nuclei—telolemma nuclei—are seen.

4. The neuraxis of the motor neuron loses its medullary sheath before piercing the sarcolemma.

*Motor endings in cardiac muscle.* No attempt will here be made to discuss the whole question of the innervation of the mammalian heart nor even to refer to the now extensive literature dealing with the subject; for this, the interested reader may consult the articles of Retzius and Berkley and especially the very recent communication by Jacques who has reviewed the literature very extensively.

We wish here simply to refer to the ultimate ending of the motor nerves on the heart muscle cells and to draw attention to a method for staining them which we believe will give more satisfactory results than the methods hitherto used. We refer here to the method used in staining the nerve ending in voluntary muscle; namely staining in methylene blue, fixing in ammonium molybdate, embedding in paraffin and sectioning, and further staining such sections in alum carmine. In heart muscle, prepared after

this manner, the nerve fibers are blue, muscle and nuclei, red. The shape and structure of the ultimate nerve endings and their relation to the heart muscle cell may, it seems to us, be more clearly made out in preparations thus prepared, than in methylene blue stained tissues fixed in ammonium picrate, or in preparations stained after the chrome-silver method.

Our results were briefly as follows:

In sections of cat's auricle from 10 to 20  $\mu$  in thickness prepared as above stated, portions of the intramuscular plexus, or pericellular plexus, described by authors are abundantly seen. The nerve fibers of this plexus are, as far as we have determined, non-medullated. They vary, however, much in size, and in the size and number of the varicose enlargements seen on them. They often show relatively large sheath nuclei, clearly seen with these stains; these nuclei stain red, the axis cylinder blue. The strands of the intra-muscular plexus may consist of single fibers or small bundles of fibers. We have now and then been able to trace such a small bundle to some one of the sympathetic ganglia situated in the wall of the auricle. Some of the non-medullated fibers of the intra-muscular plexus are therefore, no doubt, the neuraxes of sympathetic cells situated in the auricular wall. Whether they all are, or what particular intra-muscular fibers are, is a subject concerning which further research is needed. From this intra-muscular plexus, one may now and then trace a nerve fibril to its ending on a heart muscle cell. Such fibrils are usually very varicose and terminate in endings which vary in complexity. In Figs. 15 to 20, several such endings are reproduced. They may be very simple, consisting of a small terminal bulb, as shown in Fig. 15; these, it may be stated, are most numerous; or again, the fibril may branch just before it terminates, into two short filaments, each of which ends in small bulbar enlargements, as seen in Fig. 16. The endings may however be much more complex, the nerve fiber terminating in 4 to 8 small filaments, and ending in a terminal enlargement, as is shown in Figs. 17 to 20. The terminal end-bulbs in these more complex endings are usually grouped in more or less compact clusters as a majority of the figures show; they

may however sometimes be spread out over a proportionately larger area, see Fig. 20, and especially the upper cell of this figure. Sometimes it may be seen the terminal fibrils supply more than one heart muscle cell; this is indicated in Fig. 16, where the fiber sends off a small branch, ending on the cell shown, the fiber itself going on. In this way a fibril of the intra-muscular plexus may innervate four or five successive cells. Figs. 19 and 20 also show this ending of such fibrils on more than one cell. That the endings here described are on the heart muscle cell may be seen in Fig. 21, showing cross sections of heart muscle cells through the nerve ending.

We have not been able to associate these several types of endings with nerve fibers showing any peculiar or characteristic structure. Wherever it was possible to trace the fibril terminating in any one of the above described endings for some distance away from the cell on which it terminated, such a fibril or fiber always presented the appearance of a non-medullated, more or less varicose nerve fiber, the latter characteristic—the varicosity of the fiber—although very constant for non-medullated fibers, not being looked upon as showing any inherent structural differences. We are reminded here of what Dogiel has said of the structure of the ultimate branches of nerve fibers. He describes these as consisting of one or several ultimate fibrillæ, which stain deeply in methylene blue, surrounded by an interfibrillar substance, which stains only faintly in the blue; then follows this statement: “Letztere (interfibrillar substance) lagert sich in überlebendem Nervengewebe als eine gleichmässig, dünne Schicht an der Peripherie aller Nervenästchen und Fäden ab, während sie mit dem Eintritt der postmortalen Veränderungen wahrscheinlich ein wenig aufquillt und in abgesonderten Klümpchen sich ansammelt, welche sich auf dem Verlauf der genannten Aestchen vertheilen und ihnen ein charakteristisches Bild geben.” If this be so, the difference in the degree of varicosity would depend largely on the rapidity with which such terminal fibers are fixed after the removal of the “überlebend” tissue.



We have been led to mention these facts, since Berkley has quite recently described two distinct kinds of nerve fibers, with distinctive nerve endings in heart muscle. In the inter-muscular plexus, these nerve fibers are described by him as follows :

1. Varicose nerves of "longitudinal main fibers with right angled branching ; the terminations being on short ramus-cules from the finer filaments." These fibers are stained a "brownish black" in the chrome-silver method used by Berkley. "The end-apparatus of the varicose network is usually very simple, being represented almost without exception by a minute ball-like arrangement at the terminal point of the end branches."

2. Fibers that stain a "uniform jet black" and "run for a long distance with but very few side branches and exceedingly rarely develop upon themselves any knotty thickenings." "They are characterized not uncommonly by the presence of a round or elongated ball not far distant from the end apparatus." "The end apparatus of the second type of fiber, presents, in complete contrast to the fibers of the network, an end apparatus of complex form." Fig. 4, 5 and 6, of Berkley's article show these more complex endings, which are of pennate form, some simpler, others more complex. The account here given has reference to Berkley's observations on the mouse heart. In his description of the endings in the dog's heart, he states that they correspond in the main with those found in the mouse. In about 120 successfully stained sections from the heart of the dog, Berkley found about 10 endings of a more complex nature. "These expansions were of considerable size, covering the breadth of two or three muscular fibers and varied slightly in form." Berkley's interpretation of these more complex endings and also his opinion of the bulbar enlargement on the fibre thus ending, may be given in his own words: "In all these nodal structures, which are always most deeply stained, it is impossible to discover anything of a cellular nature, yet, as they are several times larger than any of the ordinary varicose knots that are met with on the fibers of the first class, and have little

that is common in appearance with them, we think, after every allowance has been made for visual error, that they may be considered bipolar cells situated in the path of the fibers, and that the end apparatus should be looked upon as their terminal expansion. However the number so far seen is too few to enable us to regard them from other than a somewhat hypothetical standpoint." As our observations were made on the cat and more particularly on the auricle, we are not fully prepared to discuss Berkley's results. We may however be allowed the following critical remarks: In the first place, in the cat at least, as our figures may show, the ultimate nerve endings in the heart muscle can not be divided into two distinct types—simple and complex; intermediate stages of complexity are found between these two extremes. Furthermore the endings described by us are all endings of varicose fibers, which, it is true, may not always show the same degree of varicosity; yet this difference is not regarded as of any essential importance, as we have above stated. The suggestion may further be made, as has been done by one of us in another place, that the nodular enlargements, which Berkely has interpreted as the cell bodies of bipolar cells, may, after all, be nuclei of the sheath of Schwann of non-medullated and not medullated fibers. When we compare the size of the nodular enlargements pictured by Berkely with the size of some of the nuclei found on non-medullated fibers, stained in methylene blue and counter-stained in alum carmine, when viewed under about the same magnification, we are led to disagree with him when he states that "this swelling in the pathway of the nerve is far too large to be thought of as a varicosity or as the nucleus of the myelin sheath of the nerve fiber, supposing such a sheath to occur in this situation."

These considerations make us somewhat skeptical as to the existence of two distinct kinds of nerve fibers with characteristic end-apparatus; and while we have no desire to discredit Berkely's observations in this direction, we can but feel that methods other than the chrome-silver method where the structure of the fiber, etc., may be determined with greater certainty, are more suitable for the investigation of this problem.

Arnstein, who first stained the cardiac muscle in methylene blue, describes their ending on the heart muscle cells without an end-bulb. "Dann sieht man den varicosen Faden sich an die Muskelzelle ansetzen ohne eine Endausschwellung zu bilden," are his words on this point. Jacques, who has quite recently reported on the heart muscle nerves as seen when stained with methylene blue, makes the following general statement concerning their ending: "From the intra-muscular fibers, terminal fibers arise, which penetrate between the cells of the muscle bundles and enter into communication with them by means of terminal and lateral branches of varied form and size, comparable for the most part to the terminations described in striped muscle of invertebrates." The endings sketched by him in Fig's. 10, 15 and 16 (young rat) and Fig. 14 (cat) of Plate XVIII, while resembling somewhat those given by us, are all somewhat coarser, showing larger end-bulbs—mushroom-like endings as stated by him—when compared with ours.

The simple ending shown in Fig. 15 resembles very closely the endings shown in Fig's. 6 and 7, Plate XV, of Retzius' article, showing the nerve ending in the cardiac muscle of the mouse when stained with the Golgi method. The more complex endings mentioned are not discussed nor diagramed by him.

Further contributions on the cardiac nerves stained with the Golgi method have been made by Ramon y Cajal and Azoulay; their results are however known to us only through reviews. Ramon y Cajal, who has stained the cardiac nerves of reptilia, batrachians and mammals, recognized a pericellular plexus, comparable to that found in smooth muscle. He states that the fibrils are devoid of myelin and beset with varicosities and attach themselves to the striated substance and end on its surface in small enlargements. Azoulay has studied the cardiac nerves in the human embryo; but reached no definite conclusion as to their ultimate ending.

*Motor endings in involuntary muscle tissue.* The endings of nerve fibers in involuntary muscle tissue have been the subject

of numerous contributions. Since their first description in 1862 by Kölliker, they have been repeatedly investigated by all the current methods. It is thought best to dispense with a review of the now somewhat voluminous literature treating of this subject, since a number of the recent writers, among whom may be mentioned Lustig, Erik Müller, Retzius, Brenheim and Schultz, have covered the ground very completely. It is now very generally believed that the nerve fibers ending in the involuntary smooth muscle tissue are the neuraxes of sympathetic neurons, situated in, or at some more remote point from, the smooth muscle in which such endings are found. Indeed quite recently, Arnstein was able to sketch an entire sympathetic neuron, the neuraxis of which terminated in the muscle tissue found in the wall of the trachea; and one of us, as stated in another place, was able to see this now and then, in the sympathetic cells found in Auerbach's plexus in some fishes and reptilia examined by him. This is, however, usually not possible, as the neuraxes and, to some extent, the dendrites also of the sympathetic neurons found in involuntary muscle tissue, are interwoven into such intricate plexuses, that the tracing of a single neuraxis through its terminal branchings becomes impossible. Many writers, following Arnold, have described three plexuses thus formed in involuntary muscle tissue,—a *ground* plexus, an *intermediary* plexus, surrounding the fasciculi or bands of smooth muscle; and an *inter-muscular* plexus found between the spindle shaped cells. These plexuses are said to anastomose with each other. There is, however, probably no actual anastomosis of the nerve fibers constituting these several plexuses, but rather an interlacement of such fibers. It is, however, not our purpose to dwell on these facts, as they may be quite readily ascertained in gold chloride, chrome silver or methylene blue preparations; but rather to discuss briefly the more disputed question of the ultimate ending of these nerves in the involuntary muscle tissue. Concerning this point, two very contradictory views have been expressed: on the one hand it is asserted more or less positively by Kölliker, Löwit and Gescheiden and in more recent years by Arnstein, Retzius, Erik Müller, Dogiel and Schultz, that



the nerve fibers terminate on the spindle shaped cells; while, on the other hand, Frankenhäuser, Lustig, Obregia and Brenheim find that the nerve fibers terminate in the muscle cell, on or in the nucleus. Arnold and Obregia go so far as to say that the nerve fibers may pass through or over the nucleus and appear again in the inter-muscular plexus (Arnold), or pass on and end in the nucleus of some neighboring cell (Obregia).

Our own results confirm the observations of those writers who contend for a free ending of the terminal fibers *on* the spindle shaped cells of involuntary muscle. Our sections were obtained from the muscular coat of the stomach and intestine of kittens, tortoises and fishes, stained in methylene blue and alum carmine, the method here being the same as used for the other motorial endings previously discussed. The sections were from 5 to 7  $\mu$  in thickness. In such sections, studied under the 1-12 oil imm., the cell outline of the spindle shaped muscle cells, as also their nuclei, may readily be made out; they are stained red; the nerve fibers, blue. Figs. 22 and 23 may serve to show the results obtained; both sketches were made from preparations obtained from the muscular wall of a kitten's stomach. Preparations made from the intestine of the tortoise and fish, show essentially the same kind of an ending, so that it did not seem necessary to duplicate the figures.

In Fig. 22, may be seen at *a*, a small varicose fibril from the intramuscular plexus. The terminal fibers of this plexus usually, as shown here, run parallel with the long axis of the muscle cells, seemingly embedded in the inter-cellular cement substance. Such terminal branches may, in sections 15 to 20  $\mu$  in thickness, be traced under a 1-12 in. oil imm., through several fields of the microscope. From place to place, short side filaments are given off from such terminal fibers, which may be traced to a muscle cell, on which they terminate in one or two nodular enlargements; one such is shown in *b*, of Fig. 22. A terminal fiber may, in this way, send side filaments to 6 or 8 muscle cells, as it courses along in the intercellular cement. Occasionally two or three short filaments end on one cell, each in a small end-bulb, as may be seen in Fig 23; this

is, however, rarely seen. That the endings are *on* the cells, and not *in* them or in the nucleus, may be ascertained in the occasional cross sections through the muscle cells and nerve endings which are here and there met, or perhaps more clearly in the oblique sections now and then obtained. See Fig. 24; also shown in Fig. 44 of Schultz's article.

These results, as may be seen from the following quotation, agree very closely with the results obtained by Müller with the Golgi method: "Die feinen Zweige endigen mit einer keulen oder birnenförmigen Anschwellung die sich auf eine Muskelzelle legt. Diese Anschwellungen sind sehr konstant und regelmässig ihrem Aussehen nach, so dass ich keinen Anstand nehme, sie als ein der Wirklichkeit entsprechendes Structurverhältniss anzusehen. Es ist indessen nicht nur an den Enden der Fäden, wo sich solche befinden. Man findet nämlich oft die Fäden ihrer ganzen Länge nach mit dergleichen kleinen Platten versehen, oft an kleinen kurzen Stielen sitzend und eine jede mit ihrer besonderen Muskelzelle in Verbindung tretend."

Schultz, who has more recently worked on the question, with both the Golgi and the methylene blue method, reaches identical results as to the ending of the motor fibers in involuntary, smooth muscle. He describes, however, another system of nerve cells and nerve fibers, which may here be briefly mentioned, although somewhat foreign to the subject in hand. Schultz states that in methylene blue preparations, he has observed a large number of nerve cells in the muscular tissue of the intestinal wall. From these, longer or shorter processes are given off, which pass out between the muscle cells. These processes show varicosities and swellings toward the end of the branches, to some extent also along the processes; these swellings and nodules are looked upon as an end-apparatus. In the more fortunate preparations, he has recognized longer processes, which are not varicose and do not branch, and which could now and then be traced into a neighboring nerve bundle. These cells, according to Schultz, form the sensory nerve supply of smooth muscle; and he states that we may find in them an explanation of the severe pain which is now and then experi-

enced when the hollow organs are diseased. Schultz seems not to be aware of the fact that sensory, cerebro-spinal nerves have been traced into the epithelium of some of the hollow organs. One of us has quite recently pictured such sensory endings in the wall of the frog's bladder, where, with methylene blue, they may be most clearly shown. And Smirnow has pointed out the existence of sensory nerves in the walls of the heart. We have no doubt that many of the larger medullated fibers which accompany the sympathetic nerves to the viscera will be proved to end in free endings in or under the epithelial lining. We are, therefore, entirely in accord with Kölliker, when he states that "Alle weit in die Peripherie entstrahlenden markhaltigen Fasern, wie z. B. die in den Milz-nerven der Weideskauer, im Gekröse des Darmes, in der Leber, u. s. w. betrachte ich als sensible Elemente." Attention needs further to be drawn to the fact that Dogiel has quite recently described a "second type of sympathetic cells" found in the ganglia of Auerbach's and Meissner's plexus, which cells are spoken of as sensory sympathetic cells. If we understand Dogiel correctly, they are not regarded as of carrying sensations of pain to the cerebro-spinal centres, but rather as functioning in local reflexes, etc. Structurally, these cells differ markedly from those described by Schultz as sensory sympathetic cells. The question may here be asked whether the cells described by Schultz as sensory sympathetic cells are not identical with the cells described by Dogiel as the "cells of Ramon y Cajal". Such cells, Dogiel states, resemble very closely sympathetic nerve cells, and stain very readily in methylene blue, and are, if one may judge from Fig's. 5 and 6 of his article, very numerous. These cells are described by Dogiel as having varicose processes; he was however unable to find processes not beset with varicose enlargements, and not branching. It is true, he adds, and we give here his own words, "Dass zuweilen irgend ein Fortsatz in Vergleich zu den übrigen feiner ersieht, mit einer grossen Anzahl Varicositäten besetzt ist und gewissermassen an einen Axencylinderfortsatz erinnert. Allein ein solcher Fortsatz unterscheidet sich dadurch scharf von einem wirklichen Axen-

cylinder einer Nervenzelle des Auerbach'schen oder Meissner'schen Geflechtes, dass er bedeutend dicker und mit varicosen Verdickungen besetzt ist ; zu dem ist er stets nach Verlauf einer oft sehr kurzen Strecke aufs neue einer Teilung unterworfen." Such cells, as Dogiel has shown by injecting the intestinal wall with gelatine, form a perivascular plexus surrounding the intestinal arteries, veins, capillaries and lymphatic vessels, and have no connection with the plexuses of Auerbach and Meissner. They are, if we understand him correctly, although he is not explicit on this point, not to be looked on as nerve cells. These cells have now and then been seen by us, especially well in some methylene blue preparations of the frog's stomach, and, in several instances, showed a very distinct granulation, the granules being relatively large and resembling very closely the granules sometimes stained in methylene blue, in cells which were looked upon as containing basophile granules. Attention must here again be drawn to the fact that not all structures staining blue in methylene blue, even when this stain is injected into the circulation of the living animal, should be looked upon as nervous in nature. This stain does stain nerve cells and nerve fibers most beautifully in some instances, leaving nothing more to be desired, yet, unfortunately, often stains other structures also, and the investigator is often at a loss how to interpret any particular preparation before him. There is, it is true, very often a slight color differentiation, which in some cases is helpful ; the nerve fibres and nerve cells staining a more purplish blue than the other tissues ; this is especially noticed in the axis cylinders of nerve fibers ; yet this statement is open to many exceptions. These facts will, we believe, explain many of the discrepancies noticed in the accounts of writers, working with similar methods and on the same tissues.

We are therefore led to agree with Dogiel in considering the cells described by Schultz as other than nerve cells, probably cells of connective tissue origin. And while we have not been able to add materially to the observations of Erik Müller, Retzius and Dogiel, and to that portion of Schultz's account which pertains to the endings of motor nerves in involuntary



muscle, we trust that our confirmation of their results with methods differing somewhat from the ones they used, may prove of some value.

*Muscle-Spindles.* In 1862, Kölliker described in the cutaneous pectoris of the frog, peculiar bundles of small muscle fibers, to which, at an expanded portion of the bundle, a relatively large medullated nerve fiber was attached. They were designated "muscle-buds" (Muskelknospen), and were regarded as showing a longitudinal division of muscle fibers and a consequent division of the muscle nerve.

In the following two years, in three communications, Kühne mentions similar structures in the muscles of adult rats, house mice, rabbits, lizards and snakes (*Coluber natrix*) and also in the frog. These structures were described by him as "muscle-spindles" (Muskelspindeln) and, while not assigning to them any definite function, he suggests the possibility of their being other than growth centers. His own words read as follows: "Sind dieselben Apparate mit einer noch unbekannten physiologischen, für den Zuckungsvorgang des Gesamtmuskels wichtigen Function, oder stellen sie nur ein Stadium noch nicht vollendeter Entwicklung einer Muskelfaser dar? Für das Letztere spricht der Umstand, dass der Spindel zuweilen bis hart an den Nerveneintritt hin Querstreifen zeigt, während für das Erstere die unverkennbare Aehnlichkeit des nicht gestreiften Abschnittes mit den Balken des Schwammgewebes vieler pseudoelektrischen Organe sprechen würde."

Since the discovery of these structures by Kölliker and Kühne, they have been repeatedly found and variously interpreted. We shall not attempt, however, to do more than give a brief summary of the opinions current in the literature concerning the muscle-spindles and similar structures. And this may perhaps best be done by classifying them as follows:

1. They have been regarded as *growth-centers*, following Kölliker in this respect, by Bremer, Felix, v. Franque, Trinchese, Tanhoffer and Volkmann, also by Schäfer and Schifferdecker. The majority of these investigators have recognized

the large medullated nerve fibers going to the muscle-spindles, but have not ascribed to them any characteristic nerve ending, and have usually regarded them as in process of division, preparatory to the innervation of the resultant muscle fibers of the spindles.

2. Other investigators, following Fränkel in this respect, who found them especially numerous in phthisical subjects and who speaks of structures very similar to the muscle-spindles as "encapsuled bundles" (umschnürte Bündel), have regarded them as pathological structures, the result of inflammatory degeneration. We may here mention Eisenlohr, who found them in cases suffering with infantile paralysis, and Millbacher, who has studied the structural changes in striped muscle in cases succumbed to one or the other of several chronic diseases. In his article, he speaks of three types of "umschnürte Bündel."

- a. Incompletely encapsuled bundles ;
- b. Completely encapsuled bundles enclosing muscle fibers plainly visible ;
- c. Completely encapsuled bundles, enclosing muscle fibers highly atrophic.

These three forms are regarded as developmental stages of one and the same process ; and the capsule is looked upon as the result of the proliferation either of the internal perimysium, or of the adventitia of adjacent blood-vessels.

Eichhorst has described muscle-spindles, or very similar structures, judging from his figures, in the striped muscle of alcoholists. He also attaches pathological significance to them in so far that he traces the development of the capsule to the greatly proliferated neurolemma of the muscle nerves, which were found markedly diseased. We may yet mention Santesson, who found, in a case of dystrophia muscularis progressiva, numerous muscle-spindles, especially in the more atrophied muscles ; they were regarded as showing an attempt at regeneration in diseased muscle. "S. Mayer and Babinski similarly ascribe them to degeneration, although considering them physiological rather than pathological, inasmuch as due to a degener-

ation of normal occurrence within active muscle." (Quoted from Sherrington.)

3. Muscle-spindles, or similar structures, have further been described by a number of writers, who have been more guarded in attaching any especial significance to them, and have described them as "physiological structures," without assigning them any definite function.

We may here mention Mays, who, in two communications, has drawn attention to them. In his first, the possibility of their being sensorial end-organs is discussed; in his second, he contents himself with the following statement: "Da ich somit die Frage, was die Muskelspindeln eigentlich seien noch nicht für entscheiden halte, so kann ich auch heute der Ansicht noch nicht unbedingt beipflichten, welche sie mit grosser Bestimmtheit als sensible Organe auffasst." Roth, who has designated them "neuro-muscular bundles" (Neuromusculäre Stämmchen), has found them in man, cat, dog, and rabbit, but ascribes to them no definite function.

Blocq and Marinesco found "neuro-muscular bodies" in atrophied muscles of poliomyelitis and polyneuritis, and have described quite accurately the capsular sheath, ascribing however no definite function to them. Pilliet has described similar structures in cases of alcoholic paralysis, amyotrophic lateral sclerosis, and progressive muscular atrophy, and draws attention to a similarity in their structure to that of the Pacinian bodies. He suggests that they may represent the end-apparatus of centripetal nerves, peculiar to striped muscle, and more easily found in atrophied than in normal muscle. Christomanos and Strössner, in a carefully prepared article, state that they were not able to satisfy themselves that the muscle-spindles were growth centres, neither could they ascribe to them any pathological significance; they are inclined therefore to regard them as a peculiar nerve end-apparatus.

4. Finally we may mention those writers who have, with more or less confidence, described the muscle-spindles as sensorial end-organs, and have, consequently, given more attention to the relation of the nerve fibers to the spindles, and to their

mode of ending. We may here mention Kerschner, who, in his first communication, mentions that he had found in connection with motor endings on the muscle fibers of the muscle-spindle, very complicated endings of the large medullated fibers which had been traced to the muscle-spindles. By reason of their resemblance to the Golgi tendon-spindles, with which they are often associated, he regards the muscle-spindles, and we may here use his own words, "als complicirte sensible Endorgane, welche den Muskel-sinne dienen dürfen."

In a second paper which appeared in the same year, he described the ending of the large medullated nerves more fully. The following is taken from his account: "The sensory fiber, or several of them (in man), divides soon after it enters the capsule, di- or tri-chotomously. The resulting branches, which may be far distant from the entrance of the nerve fibers, are wound around the muscle bundle or its individual muscle fibers; the windings above mentioned are especially numerous in man. Here and there an end-fiber can be found, which terminates in an end-bulb; the motor fiber (or several such), which may enter the capsule separately, or with the sensory fibers, runs parallel to the muscle bundle, and ends at a considerable distance from the sensory endings, in a small motor ending." Kerschner's preparations were demonstrated and described by von Ebner, at the Vienna meeting of the "Anatomische Gesellschaft" in 1892. Von Ebner here states that he concurs in Kerschner's interpretations of the muscle-spindles. About the same time, Ruffini gave an account of his observations on the nerve ending in muscle-spindles in man and cat, and gives the only figures, with which we are familiar which may be at all compared with the ones accompanying this article. (The cut given in Kölliker's text-book, showing the ending of a nerve in the muscle-spindle of a rabbit, seems to us sketched from an incompletely stained preparation.) Ruffini makes this statement concerning the ultimate ending of the nerve fibers on the muscle fibers of the spindle: "J'ai pu ramener ces terminaisons finales de la fiber nerveuse à trois types principaux, que j'appellerai terminaisons à anneaux, à spirales et à fleurs." His ac-



count of these endings will be more fully considered subsequently. In still another article, Kerschner reiterates his former views as already given, and, while giving a summary of the literature appearing before that time, adds little to what he had stated concerning the ending of the nerve fiber in these structures. Kerschner here, however, promises an extensive monograph on the sensory endings in muscle and tendon-spindles, with numerous plates. This, if it has appeared, we have not been able to consult, as we have not found any reference to it.

Sherrington deserves the credit of having conclusively shown, by experimental means, that the nerve fibers going to the muscle-spindles are sensory. We quote from him as follows :

“ My own experiments have been suitable for examining the effect of degeneration of the motor spinal roots upon the nerve fibers supplying the muscle-spindles ; they demonstrate that the muscle-spindle is supplied with nerve fibers arising in cells of the spinal root-ganglion. In muscles from which all motor fibers have been entirely removed by degeneration I have never in a single instance failed to find every spindle met with in the muscle still possessed of perfectly sound myelinate nerve-fibers. The myelinate fibers are traceable from the sensory roots, and penetrate into the spindles and terminate within them. The muscle-spindle proves therefore to be a sensorial organ as argued by Kerschner and as indicated by the histological analysis of the nerve-ending by Ruffini.”

We may further mention Dogiel's work, who has described very accurately the endings of the spindle-nerves in the muscle-spindle of the frog, as seen when stained with methylene blue ; he, while mentioning that the spindle-nerves have no connection with the motor nerves of the muscle, dismisses his account without making any statement as to the probable function of the muscle-spindles. Sihler, who has quite recently worked on the ending of the spindle-nerves in the muscle-spindle of snakes, defends the view that this is a sensorial end-apparatus which subserves the muscle sense.

Our own observations pertain more particularly to the ending of the spindle-nerves in the muscle-spindles. The method used by us was selected with this end in view; the method, while showing the general structure of the muscle-spindles, was not the method which would have been selected, had this been the more particular aim of the research. Our observations on the general structure of the muscle-spindle confirm, in the main, observations previously made, and more particularly those made by Sherrington and given in his account of these structures; this account will here be followed.

*Capsule of muscle-spindle.* The capsule or perimysial sheath of some writers, has essentially the same structure in all vertebrates examined, although it varies much in thickness. It may be said to be made up of concentrically arranged layers of white fibrous tissue, the several layers being often in close apposition, or again more or less distinctly separated one from the other, leaving larger or smaller clefts between them. The number of these concentric layers varies; Sherrington places it at six to eight, which number holds good for many of the muscle-spindles seen by us, especially those found in mammalian muscle. In amphibia, reptilia, and birds, the capsule of the spindle may be said to be relatively thinner, consisting often of only two to four concentric layers; thicker capsules are, however, also met. The fibrous tissue of the concentric lamellæ is white fibrous, practically devoid of yellow elastic tissue. This may be seen in muscle-spindles overstained in methylene blue, our experience having taught us that in tissues thus overstained, the yellow elastic fibers are often clearly brought out; it is also seen in sections stained after Unna's method; neither of these methods shows any elastic fibers in the capsule of the muscle-spindle. At the beginning of the muscle-spindle (proximal end), the capsule becomes continuous with a somewhat thickened perimysial sheath, which surrounds the muscle fibers about to enter the muscle-spindle. The behavior of the capsule at the distal end of the muscle-spindle depends somewhat on its relative position in the muscle. The spindle may be embedded in the muscle substance, in which case, as Sherrington

correctly states, "its long axis lies parallel to the muscle fibers amid which it is embedded;" here the distal end of the capsule seems again to become continuous with the internal perimysium. This, it would seem, is the more usual disposition of the distal end of the capsule in amphibia and reptilia, and is now and then found in birds and mammalia.

In case the muscle-spindle lies near the tendinous insertion of the muscle, in which case the long axis may also be parallel to the muscle fibers amid which it is embedded, or may be at an angle to them, the distal end of the capsule becomes continuous with the fibrous tissue septa, or with the tendon; this we have found to be the more common ending of the spindle-capsule in mammalia, but has been seen also in birds and reptilia (tortoise).

More immediately surrounding the enclosed muscle fibers, designated by Sherrington as "*intrafusal fibers*," there is found a connective tissue sheath which he has described as the "*axial sheath*," consisting of thin bands or plates of white fibrous tissue in which nuclei are numerous.

Between the capsule and the axial sheath is found a relatively large lymph space—Golgi and Sherrington—designated by the latter as the "*periaxial space*;" this, he correctly states, is "bridged across and partially subdivided in many points by extremely tenuous membranes and filaments." The periaxial lymph space is broadest near the middle of the muscle spindle, generally tapering off toward the ends. The intrafusal fibers are sometimes in the middle of this space and again eccentric. The space also shows buddings here and there, which seem, however, in a large measure due to foldings in the capsule, the result of contraction of the contiguous muscle fibers.

*Intrafusal muscle fibers.* The intrafusal muscle fibers differ in size and structure from the muscle fibers of striated muscle. Their number varies. In the snake, only one intrafusal fiber is found, as has been stated by Kühne, Mays, and Sihler; similar spindles have been found in the lizard by Bremer, Trinchese and Cattaneo. In the other vertebrates examined, the number varies from two to ten, and, as Sherrington has stated, in some of



the larger spindles—compound spindles—as many as twenty may be found. It is stated (Sherrington) that the muscle fibers destined to form intrafusal fibers are of the red variety, rich in protoplasm. In muscle-spindles containing more than one intrafusal fiber, one, two, three, and perhaps even more muscle fibers enter the proximal end of the spindle, and at once divide into two, three, or even four daughter fibers, of round or oval shape; these are the intrafusal fibers. They usually have a more or less parallel course in the spindle, although in longitudinal sections, they now and then give the appearance of a loose braid, showing that the intrafusal fibers may now and then be more or less twisted in the spindle. The intrafusal fibers are, so far as our observations allow us to assert, enclosed in a sarcolemma, although this is not always distinctly made out in sections, and Sherrington states that “some of the intrafusal fibers are devoid of sarcolemma.” The intrafusal fibers show a more or less distinct longitudinal and cross striation, which may usually be made out through the entire length of the fiber. In the middle third of the spindle, the portion described by Sherrington as the equatorial region, the intrafusal fibers possess, according to this observer, the following structure: “The intrafusal fiber often becomes somewhat smaller in diameter and is nearly always circular in section. Its surface zone soon gets thickly encrusted with or almost completely occupied by a sheet of nuclei. Whether these nuclei are strictly part of the muscle fiber is not clear to me. The nuclei are spherical or slightly oval, are clear, and measure about  $6\mu$  in diameter. Cross-sections reveal beneath the nuclear sheet a thin tubular layer which is fibrillated. This tubular layer itself invests a central core ( $4\mu$ - $5\mu$ ) of hyaline substance, which runs rod-like along the axis of the intrafusal fiber in this region. The cross-section of the fiber thus often displays a nearly complete zone of four to six nuclei around a hyaline centre.” We have quoted thus freely from Sherrington’s account, because our own observations are not fully in accord with what he has here described. The sheet of nuclei mentioned by him, is not, we believe, a part of the intrafusal muscle fiber, as, in instances where it was possible to



make out a sarcolemma on the intrafusal fibers in the equatorial region of the muscle-spindle, the nuclei above referred to, seemed outside of this sheath. They seem to belong to a connective tissue sheath, which surrounds each intrafusal fiber; a sheath inside of the axial sheath, with which it is partly fused, or to which it may be partly united by means of bands or septa of fibrous tissue. In longitudinal sections of muscle-spindles, the arrangement of the nuclei is such that they seem to belong to endothelial cells lining the fibrous tissue sheath surrounding the intrafusal fibers. On this point, however, we possess no conclusive observations. The hyaline core mentioned by Sherrington, we have interpreted as sarcoplasm, the intrafusal fibers, especially in the equatorial region, often showing fibrillation only in the peripheral zone. In the central of the intrafusal fibers, also more apparent in the equatorial region, a row, or sometimes two parallel rows of nuclei are found. We can confirm the statement of Christomanson and Strössner, of Kerschner and Sherrington, that these nuclei are resting nuclei, which show no sign of karyokinetic cell division. The main differences which we have observed between the structure of the intrafusal fibers in the equatorial region and that in the other parts of the spindle—proximal and distal polar regions—are that in the former, the cross and longitudinal striation is not so apparent, the central "hyaline core" is more clearly made out, and the nuclei are more numerous. The intrafusal fiber in the equatorial region resembles in structure a developing striated muscle fiber. In cases where the muscle-spindle is situated near the tendon of the muscle or near a fibrous septum, the intrafusal fiber becomes tendinous and seems to fuse with the distal part of the spindle capsule. In the simpler muscle-spindles, containing one intrafusal fiber, this becomes less distinctly striated and shows more nuclei, when within the spindle. In the snake, the muscle fibers destined to become intrafusal fibers are throughout very much smaller than the other striated muscle fibers, about 8 to 10 times smaller, as correctly stated by Sihler. After entering the spindle, it may retain its former size or become slightly larger, less distinctly striated and show more

nuclei, the nuclei being found in an axial core, not striated and probably sarcoplasmic in nature. The capsule of these simpler spindles consists of two to three concentrically arranged membranous lamellæ of fibrous tissue, between which clefts or spaces may now and then be made out. These lamellæ are not, we believe, elastic in nature ("mehrere Lagen elastischer Membranen"), as Sihler has stated.

We may finally refer to the fact that the muscle-spindles have, according to Cattaneo, a distinct blood supply. One or two relatively large vessels go to each spindle. The vessels pass along the border of the spindle either on or in the capsule and give off branches which have a spiral or wavy course. Our own observations on this point are confined to the muscle-spindles found in the rabbit. In relatively thick sections of one of the intrinsic plantar muscles previously injected with gelatine blue, these spindle-vessels may readily be seen. From the larger branches found in the capsule of the spindle, secondary branches are given off, which have a spiral or wavy course and anastomose to form an open network surrounding the spindle; from this, relatively long, straight branches may be traced between the intrafusal fibers of the spindle.

*Spindle-nerves.* Nearly all writers who have given observations on muscle-spindles, have recognized large medullated nerve fibers going to these organs, and have described a branching of these nerve fibers, either before entering the spindle, or after their entrance. Sherrington, as previously stated, was the first to show conclusively that such fibers are spinal ganglion—sensory—fibers, which do not degenerate when all the motor nerve fibers going to the muscle have been removed. We find his account of the general distribution of the spindle-nerves very accurate and applying not only to the mammalia studied by him—cat and monkey—but also, with very little modification to other vertebrates possessing muscle-spindles containing more than one intrafusal fiber. As he has stated, usually more than one large medullated fiber, " $7\ \mu$ — $18\ \mu$ " (or even longer) in diameter, is distributed to one spindle; two to four may be given as the number for the smaller spindles and five to eight

for the larger spindles—compound spindles. The number seems often, however, greater in the immediate vicinity of the larger spindles, due to the fact that now and then, one or the other of the large medullated fibers going to a spindle branches at a very acute angle at some distance from the muscle-spindle. The fibers may approach the muscle-spindle singly, in which case, as is well known, they are surrounded by a thick sheath of Henle, or in small bundles enclosed in a thick connective tissue sheath. The nerve fibers usually enter the spindle from the side, in the smaller spindles, near the center, slightly toward its proximal end, though in the larger compound spindles (see Fig. 39) some of the fibers may enter near the proximal end. In the tortoise now and then, and in the snake more generally, the spindle-nerves enter at the proximal end of the spindle. A portion of Henle's sheath of the spindle-nerves, or of the fibrous-tissue covering of the small bundles of such nerves, becomes continuous with the capsule of the muscle-spindle. Within the capsule, the still medullated nerve fibers, which cross the periaxial space usually obliquely to reach the axial portion of the spindle, are also surrounded by a connective tissue sheath (Henle's sheath), containing many nuclei, which becomes continuous with the axial sheath, where the nerve fibers penetrate it. The course of the spindle-nerves in the periaxial space varies. They may pass obliquely across the periaxial space to reach the axial sheath, which they may penetrate at once or along which they may run for a short distance before penetration; they may have a serpentine course in the periaxial space and may be spirally wound around the axial portion of the spindle. The spindle-nerves remain medullated until they have penetrated the axial sheath, within which they may lose the medullary sheath soon after passing through the axial sheath, or may run along a longer or shorter distance between the intrafusal fibers, having a straight, serpentine, or spiral course, before they lose the sheath of myelin. It has above been intimated that the medullated fibers going to the muscle-spindles may branch; our own observations on this point, as also those on the structure of the spindle nerves, are wholly in accord with



the statements regarding these points made by Sherrington; we may therefore give here his words: "I have seen spinal-ganglion fibers branch both when close outside and when quite within the thickness of the capsule. The branching is usually by dichotomous division at a node of Ranvier, and the angle of divergence of the two branches is usually quite small. While approaching the spindle the length of the sheath segments (internodes) of the spinal-ganglion fiber is from  $600\ \mu$  to  $900\ \mu$ ; at a variable distance within the spindle [We also find before the spindle nerve pierces the capsule], the segments suddenly become much shorter,  $80\ \mu$  to  $130\ \mu$ . At the same time, dichotomous subdivision becomes much more frequent, the myelin-sheath becomes much less thick, and the diameter of the axis cylinder considerably greater, e. g.  $14\ \mu$  instead of  $9\ \mu$ ." The ultimate ending of the spindle-nerves, i. e. the ending of the non-medullated branches of the intrafusal portion of the spindle-nerves, may best be described separately for each of the classes of vertebrates studied. They have, however, this in common: the ultimate endings of the non-medullated branches of the spindle-nerves are found outside of the sarcolemma surrounding the intrafusal fibers, between this sheath and the connective tissue sheath which, as above stated, surrounds each intrafusal muscle fiber.

*On the ultimate ending of nerve fibers in muscle-spindles. Amphibia.* Our preparations were made from muscle-spindles found in the *cutaneus pectoris*, *port. sternalis anterior* and *posterior* of *m. pectoralis*, and the *sartorius*. Especially in the first named muscle, which so far as we may judge, contains from 4 to 5 muscle-spindles, the spindle-nerves may be readily stained in methylene blue. Some of the preparations thus obtained were fixed in ammonium picrate and mounted in glycerine-ammonium picrate; others were fixed in ammonium molybdate, embedded in paraffin and sectioned. Dogiel has described and sketched the ending of the spindle-nerves in the muscle-spindles of the frog. A comparison of Fig. 8 of his article with our Fig. 36, shows that we have corroborated his observations. One, two, or even three large medullated fibers are distributed



to each muscle-spindle. Occasionally, while yet outside the capsule, more often in the periaxial space, the spindle-nerves undergo branching; the resultant branches consist of one, two, three, or even more, short internodal segments. These branches course along the surface of the axial portion of the spindle, in part outside, in part within the axial sheath and may here have a straight or serpentine course or may be partly wound around the axial portion of the spindle. Within the axial sheath, the medullated nerve fibers may lose their medullary sheath at once or after passing a longer or shorter distance between the intrafusal fibers, where they may undergo further branching. The non-medullated continuations of the medullated nerve fibers break up into fine fibers, richly beset with large varicose enlargements. These, the terminal branches, are in contact with the intrafusal muscle fibers, along which they extend for longer or shorter distances and may often be traced to the poles of the muscle-spindle. In longitudinal sections of muscle-spindles, Fig. 25 (double stained in methylene blue and alum carmine), but especially in cross section, Figs. 26 and 27, it may readily be seen that these terminal fibers are just outside of the sarcolemma of the intrafusal fibers, between it and the connective tissue sheath surrounding these fibers.

*Snake.* Our preparations showing the nerve endings in the muscle-spindle of the snake were made by injecting the methylene blue (1% solution in normal salt), through the heart. Strips of the back muscles, in which, as Kühne and Sihler have shown, muscle-spindles may be found, were removed to a slide. In these ribbon-like muscles, a muscle-spindle showing a stained spindle-nerve may now and then be found; and we were thus able to obtain a number of muscle-spindles showing the ending of the spindle-nerves. The muscle-spindles of the snake and lizard, as previously stated, are simple, containing only one intrafusal muscle fiber, surrounded by a capsule and axial sheath. One, or, at the most, two medullated nerve fibers have been traced to such a spindle, and, in the preparations obtained by us, the nerve fiber usually enters the spindle at one or the other pole. If two nerve fibers go to the same spindle, these,

in the few instances seen by us, enter by opposite poles. In Fig. 37, may be seen such a muscle-spindle receiving two nerve fibers; these, as may be seen, approach the spindle in two quite distinct nerve trunks. (In the figure, only the intrafusal muscle fibers and the nerve fibers are shown. The sketch is from a methylene blue preparation, fixed in ammonium picrate and cleared in glycerine-picrate. In the preparation, the fibrous capsule, as also the fibrous connective tissue sheath around the nerve fibers continuous with the capsule, could be made out, although not very distinctly; also the fact that in the portion of the intrafusal fibre not distinctly striated in the figure, there were about 10 or 12 nuclei. It was, however, found that if all these structures were reproduced in one figure, the ultimate ending of the nerve fibers, which we hope here to show more especially, would come out indistinctly by reason of the fact that it would be covered up by nuclei, etc.) The medullated spindle-nerves lose their medullary sheaths soon after entering the capsule; the ultimate endings are therefore non-medullated, and are, we believe, under the axial sheath in contact with the intrafusal fiber. We have not been able to make longitudinal or cross sections of the muscle-spindles of the snake; the number of successfully stained endings was not sufficient to admit of this. Yet in optical sections of the spindles, a connective tissue sheath, inside of the capsule, which we regarded as the axial sheath, seemed to be outside of the ultimate ending of the nerve fibers.

The ultimate ending of the spindle-nerve is as follows:

The non-medullated continuation of the spindle-nerve divides, soon after its entrance, into two or three branches; these branches may be traced on the intrafusal muscle fiber for some distance, giving off in their course band-like offshoots, which may partly enclasp the intrafusal fiber (*a*, Fig. 36), or almost completely encircle the intrafusal fiber (*b*, of the same figure); the fiber itself ending in one or two large disc-like expansions, *c*, of the figure. The non-medullated fiber, before giving off the band-like offshoots above mentioned, may present one, two, or three flattened expansions, of round, oval, or spindle

shape, as may be seen in the figure. The ultimate endings of the spindle-nerves in the muscle-spindles of the snake seen by us, do not all present the same configuration; yet the type is essentially as above described. Sihler, as he himself has stated, was not able to make out clearly the ultimate ending of the nerves in the muscle-spindle of the snake; in some few instances, however, he was able to make the following observation: "Es giebt nämlich auch Spindeln, wo die Querstreifung des Muskels im Spindelmantel nicht verloren geht, wo bloss im inneren des Muskels ein Streifen der dunkeln Substanz sich findet. In solchen—freilich seltenen—Spindeln konnte ich mehrere feine Nervenweige von myelinhaltigen Nerven abgehen sehen, und glaube ich kaum, dass optische Schnitte der *Henle'schen* Scheiden mich getäuscht haben." The nerve fibers mentioned by Sihler may be the branches of the intrafusal, non-medullated fibers above referred to, his stain not bringing to view the ultimate endings. Other writers, who have given observations on the simple muscle-spindle—designated by Kerschner as "Kühnische Organe"—(Kühne, Bremer, Mays, Trinchese and Cattaneo) have given no definite observations on the ending of the spindle-nerves.

*Tortoise.* The preparations of muscle-spindles made from these reptiles, were obtained from the vasti muscles. A one per cent. solution of methylene blue in normal salt was injected into the abdominal aorta, and the muscle exposed about an hour after the injection, cut into strips and placed on a slide and examined from time to time, until the endings of the spindle-nerves seemed stained. The tissues were either fixed in ammonium molybdate and sectioned, the sections being further stained in alum cochineal, or were fixed in ammonium picrate and teased, cleared and mounted in glycerine-picrate. The general structure of the spindles is very much as previously described. The intrafusal muscle fibers, from two to eight in number, are surrounded by an axial sheath, periaxial lymph space and capsule, each intrafusal fiber being further surrounded by its own connective tissue sheath, which is partly fused to the axial sheath, or connected with it by bands or septa of fibrous

tissue. In the tortoise, many of the muscle-spindles are compound, showing more often two, occasionally three areas of nerve distribution. One, two, or three large medullated nerve fibers go to the smaller muscle-spindles, or to each area of nerve distribution in the compound spindles. The spindle-nerves are surrounded by a sheath of Henle, which (see Fig. 28 and 30) becomes continuous with the capsule and with the axial sheath. The spindle-nerves are medullated until they are within the axial sheath, and also show the short internodal segments, mentioned by Sherrington for mammalia, as previously quoted. Once within the axial sheath, they soon lose their medullary sheath, may now undergo further branching, and may be traced for longer or shorter distances by the side of, or between the intrafusal fibers. The ultimate ending is on the intrafusal fibers, outside of the sarcolemma, but within the connective tissue sheath surrounding the intrafusal fiber. This may be seen in Figs. 29 and 30. The configuration of the ultimate ending of the non-medullated end-branches of the spindle-nerves is shown in Fig. 28, a portion of a compound muscle-spindle of *Emys meleagris*, stained in methylene blue and alum cochineal. In this figure, the ending of the non-medullated fiber (terminal branch of a spindle-nerve) designated by  $\alpha$ , may be regarded as typical. These endings are somewhat difficult to describe and may perhaps be best understood by reference to the figure. They may be likened to a strip of paper, which has, from place to place, been cut nearly in two, the various paper segments thus produced being further trimmed and scalloped into irregular, triangular, oval, or spindle-shaped forms, which are connected by narrow uniting bridges; the whole ending, as thus described, has a somewhat serpentine course on an intrafusal muscle fiber, the irregular, broader portions being moulded to the side of the intrafusal fiber. Only one complete ending is shown in the figure above referred to, and portions of other endings; this is inevitable in sections.

In preparations of muscle-spindles stained in methylene blue, fixed in ammonium picrate and teased, cleared and mounted in glycerine-picrate, it may be seen that a spindle-nerve may



have several, two, three or four, or perhaps even more such endings; and these are not always on the same intrafusal fiber, the non-medullated branches going to this or that intrafusal fiber before ending.

*Birds.* Our observations on the muscle-spindles of birds are confined to the dove, and the muscles more particularly studied were several small muscles on the posterior surface of the metatarsus. A 1 % solution of methylene blue in normal salt was injected into the aorta; the muscle exposed about one hour after the injection and observed from time to time until the spindle-nerves seemed completely stained. The tissues were fixed in ammonium molybdate, embedded in paraffin, and cut longitudinally and transversely, the sections being further stained in alum cochineal. We may here add that we have found the methylene blue method somewhat unsatisfactory for staining the endings of the spindle-nerves in birds. For some reason which we can not-at present explain, it seems to stain the nerve endings in birds less readily than in the other vertebrates we have examined.<sup>1</sup> It is usually necessary to expose the previously injected muscle pieces quite a long time to the air, sometimes 30-45 minutes, before the blue color develops in the axis cylinders and their endings; as a result, the muscle fibers and other structures of the muscle are often stained quite deeply blue, before the nerve fibers are properly stained. In some few instances, however, what we have regarded as a successful stain of the endings of the spindle-nerves has been obtained, and the observations here given are based on such preparations. The general structure of the muscle-spindles of birds is as has been previously described. They contain from two to six relatively small intrafusal fibers; these are surrounded by an axial sheath, periaxial space, and a capsule consisting of three to five concentric layers of fibrous tissue. The intrafusal fibers are further enclosed, each in a separate, thin, fibrous tis-

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<sup>1</sup> In some of our later work we now and then found that the nerve fibers were stained a very short time after the removal of the tissue; but also found that such stained fibers bleached very quickly. This may be an explanation as to why we so often failed in staining the spindle-nerves in the bird.

sue sheath; this sheath and the axial sheath contain many nuclei. Many of the muscle-spindles of birds seen by us have only one area of nerve distribution, but now and then those with two areas have been found. One, two, or three medullated fibers are distributed to each of the smaller spindles or to each area of nerve distribution in the larger—the compound spindles. They are surrounded by a sheath of Henle, which ends, partly in the capsule and partly in the axial sheath. The branching, course, and structure of the spindle-nerves in the bird is as previously described in discussing in a general way the spindle-nerves, and need not here be repeated. They lose their medullary sheath within the axial sheath, the non-medullated continuation of the spindle-nerves now and then subdividing into two or three branches. The ending of such non-medullated branches is shown in Fig. 31; the fiber *a*, presenting, we believe, a typical ending. As may here be seen, the axis cylinder (non-medullated terminal branch) ends in an irregular expansion resting on the intrafusal fiber; from this, processes which resemble somewhat a repeatedly folded ribbon are given off. These processes show successive broader expansions of round, oval, or irregular shape, united by narrower bridges, and extend for some distance on the intrafusal fiber. In preparations of the whole spindle or in longitudinal sections of a spindle, these processes are seen on the intrafusal fibers, in optical section by the side of the intrafusal fiber (*b* of Fig. 31), and also under the fiber. The ending therefore surrounds the intrafusal fiber. Now and then, the non-medullated terminal branches of the spindle-nerves break up at once into two or three processes having the above structure, or, apparently, may continue into such a process; the latter condition may however be due to imperfect staining.

In birds also, a spindle-nerve may have an ending as above described, on more than one intrafusal fiber; on as many as three fibers; that these endings are outside of the sarcolemma may be seen in Fig. 32, a cross section of a small muscle-spindle of a bird, stained in methylene blue and alum cochineal.

They are within the connective tissue sheath surrounding each intrafusal fiber.

*Mammalia.* In mammalia we have stained the nerves going to muscle-spindles in the dog, cat, rabbit, Guinea pig, and rat, and lately we have confined our attention to the spindles found in the intrinsic plantar muscles, where, as Sherrington has stated, they are very plentiful. The spindle-nerves were stained by injecting a 1 % solution of methylene blue in normal salt into the abdominal aorta, after bleeding the animal. The intrinsic plantar muscles were exposed about one hour after the injection, removed to a slide and observed until the nerve endings seemed stained; the tissues were fixed in ammonium molybdate and sectioned in paraffin, the sections being further stained in alum carmine or alum cochineal; other muscles were fixed in ammonium picrate, teased, cleared, and mounted in glycerine-picrate. The former method brings out very clearly the relation of the ultimate ending of the spindle-nerve to the intrafusal fibers; the latter, the course and the structure of the spindle-nerves as they approach the spindle, as also their general distribution in the spindle.

In all mammalia examined by us, muscles with only one area of nerve distribution and those with several areas in which spindle-nerves terminated—compound spindles—were found. The latter were more numerous in the dog, cat and rabbit than in the smaller mammals—Guinea pig and rat—examined by us. In the dog, several very large muscle-spindles were found, having as many as four areas of nerve distribution.

The general structure of the muscle-spindles of mammalia, as also the distribution and structure of the spindle-nerves, has been discussed in the preceding pages. We may here, however, reiterate the following points regarding the spindle-nerves:

From one to four large medullated nerves end in the smaller spindles and from five to eight in the larger, compound spindles.

Single spindle-nerves are surrounded by a thick sheath of Henle; small bundles of spindle-nerves, by a connective tissue sheath, which becomes in part continuous with the capsule, in

part, with the axial sheath. The spindle-nerves remain medullated until they are within the axial sheath, the internodal segments becoming shorter as the muscle-spindle is approached; but this is more especially noticeable after they have penetrated the capsule. After losing the medullary sheath (within the axial sheath), the non-medullated continuation of spindle-nerves undergoes further subdivision, before the ultimate ending is reached. The general course and structure of the spindle-nerves may be seen in Fig. 39, a sketch of a compound muscle-spindle from the intrinsic plantar muscles of a dog, stained in methylene blue and fixed in ammonium picrate, teased and cleared in glycerine-ammonium-picrate. See also Fig. 38, a smaller spindle, also from the dog, and prepared in the same way. In both the figures, only the intrafusal fibers, with the spindle-nerves and their endings are shown. Observations on the ultimate ending of the non-medullated terminal branches of the spindle-nerves have been made by Kerchner (who mentions in his account observations on man, cat, rabbit, rat, and mouse) and by Ruffini (man and cat) and by Kölliker, who mentions briefly and diagrams the ending of a spindle-nerve in the muscle-spindle of a rabbit. The observations of these investigators were made on tissues stained in gold chloride, and, while we are not able to add materially to the accounts which Kerschner and Ruffini have given, yet, as our observations were made on tissues stained in methylene blue, and, to some extent (cat and rabbit) on tissues stained in methylene blue, fixed, sectioned and double stained in alum carmine and cochineal, we may here present our results as corroborative evidence.

Ruffini, whose account we may here follow (as the few figures he gives are the only ones with which we are familiar, comparable to the ones given by us), describes for the cat, three types of ultimate endings of the spindle-nerves—spiral, circular, and flower-like endings (“*terminaisons à spirales, à anneaux, et à fleurs*”). Of these, the spiral endings may be first considered, as they seem to us the most typical. The non-medullated terminal branch of the spindle-nerve thus ending, flattens out



into a ribbon-like ending, more or less irregular, which is spirally wound around the intrafusal fiber, this spiral extending for a longer or shorter distance along the intrafusal fiber; the spiral turns are sometimes so close together that they almost touch each other, or again, farther apart, so that they can be clearly made out. This mode of ending may be seen at *a*, in Fig. 38 and also in various places in Fig. 39. These spirals have also been described by Kerschner, who very correctly adds that from place to place offshoots proceed from the spiral, which may end on the intrafusal fiber surrounded by the spiral, or on some contiguous intrafusal fiber. The "ring shaped" endings of Ruffini have, we believe, been correctly interpreted by Kerschner, when he states: "Die meisten der 'ringförmigen Endigungen' Ruffini's entsprechen Seitenansichten flacher Spiralwindungen." Such ring shaped endings may however now and then be formed by short side branches of the non-medullated terminal branches, which almost completely, or completely, encircle an intrafusal fiber; several such endings may be side by side on an intrafusal fiber. (See *b*, of Fig. 38.) The flower-like endings mentioned by Ruffini, are, no doubt, as suggested by Kerschner, the terminal endings of the spirals, or of branches from the spirals; they may, however, now and then be seen as branches from the terminal, non-medullated continuation of the spindle-nerves, which have a zigzag course on an intrafusal fiber without forming a spiral; see *f* of Fig. 39. In the rat, Guinea pig, and rabbit, spirals are not so apparent as in the dog and cat above described. One, two, or three spiral turns of the ending may now and then be seen. The endings of the non-medullated terminal branches of the spindle-nerves, are, in the rabbit, Guinea pig, and rat not so ribbon-like as in the dog and cat, are much more irregular—"knorrig oder knotig" as Kerschner expresses it, and are much more given to subdivision. We give in Fig. 33, a portion of a compound muscle-spindle of a rabbit. This spindle has three areas of distribution; one (to the left of the figure), and a portion of another (to the right of the figure) are shown in the section from which the sketch was made, the third is in the succeeding section of the series. As may be seen in

the figure, no distinct spirals are here shown, the ending consisting of broad, irregular main stems resting on the intrafusal fiber, from which side branches are given off which partly or completely encircle the intrafusal fibers.

That the endings, as above described, are outside of the sarcolemma of the intrafusal fibers may be seen in Figs. 34 and 35; they are, however, within the connective tissue layer surrounding each intrafusal fiber. Spindle-nerves may end on more than one intrafusal fiber, as is shown in Figs. 33, 38 and 39, and especially well shown in Fig. 34, a sketch of a somewhat oblique section of a large muscle-spindle of a cat. The large medullated fiber shown in this figure divides into two non-medullated branches, one of which may be traced to five relatively small intrafusal fibers.

It needs to be stated, however, that, while a spindle-nerve may end on several intrafusal fibers (on an average 3 or 4), other spindle-nerves going to the same area of nerve distribution, or to other areas in the compound spindle, may and often do end on the same intrafusal fibers. Figs. 38 and 39 may serve to show this. In some of the larger muscle-spindles containing 12 to 15 intrafusal fibers, a number of spindle-nerves end in one area of nerve distribution, surrounding three, four, or five intrafusal fibers in one portion of the spindle, another small bundle of spindle-nerves ending on another group of intrafusal fibers in another portion of the spindle; the whole spindle being surrounded by one capsule.

We have not found opportunity to investigate the endings of spindle-nerves in the muscle-spindles of man. That these structures are present in man has been abundantly shown. Investigators who have regarded them as pathological structures have worked on human material, and the figures they give leave no room for doubt as to the identity of the structures they have described, with what has been described as muscle-spindles in other vertebrates. Kerschner and Ruffini have studied the nerve endings in muscle-spindles of man with the gold chloride method. They both state that the annulo-spiral endings are not found here. The ending seems compact, and from what

may be gathered from their brief descriptions, it may resemble the endings found in the rabbit.

Sherrington asks the following question: "Is the intrafusal muscle, like the rest of the muscle, connected directly with motor nerves?" In attempting to answer this question with the gold chloride method, he states that he was unable to find motorial end-plates on the intrafusal fibers. He found, however, that by degenerating *all* the nerves going to a muscle (cutting the sciatic nerve of a cat under the gluteus muscle), the striated muscle-fibers of the gastrocnemius and intrinsic plantar muscles were completely degenerated, while the intrafusal muscle-fibers were not altered from their normal. He further states: "The intrafusal fibers seem in regard to their nutrition to be largely independent of both the afferent and the efferent nerves of the muscle, if one may judge by absence of obvious degeneration in them for five months after total enervation." On the other hand, Kerschner finds, as previously quoted, that the intrafusal fibers possess a motorial ending. He states: "Der motorische Nervenfaden (oder mehrere solcher) welcher gesondert oder mit den sensiblen Fasern eintritt, läuft eine Strecke weit mit dem Muskelbündel parallel und endet in ziemlicher Entfernung vom sensiblen Endapparate mit kleinen motorischen Endgeweißen." In a number of instances, we were able to find what we have interpreted as motorial endings on the intrafusal fibers; *m. c.* in Fig. 37 and 39, show such endings. More often, have we found medullated nerve fibers, smaller than the spindle-nerves, accompanying them to the spindle, but usually they could not be traced to the endings. These may have been motor fibers. We are inclined therefore to agree with Kerschner, that some of the intrafusal fibers at least have a motorial ending. The ones we have found, were, so far as we now remember, always distal to the sensory ending—the ending of the spindle-nerve.

We may further mention that we have, now and then, in rare cases, found sympathetic nerve-fibers in the capsule of the muscle-spindles. These are shown in Figs. 38 and 39, *s. n.* They are, no doubt, vaso-motor fibers of the spindle vessels, as such fibers are now and then seen in muscle-spindles double

stained in methylene blue and alum carmine or cochineal, where they are in the immediate vicinity of vessels, or in a vessel wall. This may be seen in Fig. 34, *s. n.*

In closing this account, we may briefly refer to the probable function of these muscle-spindles. What we may have to say on this point has been implied in the preceding pages in discussing the endings of the spindle-nerves. Our observations have been entirely histological. That the muscle-spindle is a sensorial end-organ, situated in voluntary muscular tissue, there seems to us to be no doubt. The general structure of the spindle-organs, their rich nerve supply, and the distinctive ending of the spindle-nerves, would alone, it seems to us, warrant such a conclusion; this seems to us fully substantiated in Sherrington's observations showing that the spindle-nerves are spinal root ganglion nerves.

It has been suggested by Kerschner and Sihler, no doubt on *a priori* grounds, that the spindle-organs may have to do with the muscle sense. Sherrington has shown that under a large aponeurosis, belonging to the distal portion of the vastus medialis, spindle-organs are numerous. He states: "If this aponeurosis be thoroughly separated, however carefully, I have always found the 'knee-jerk' irrevocably lost from the muscle."

A study of the structure of the spindle-organs (we refer here more particularly to their capsule, peri-axial lymph space, etc.) and their resemblance in these respects to other sensorial end-organs—Pacinian and Herbst corpuscles—causes us to agree with Sherrington when he states: "That the stimulus to which these organs are especially adapted is mechanical in quality."



ADDENDUM. Since the completion of the manuscript for the foregoing contribution there have appeared a number of articles on the subject of the muscle-spindle. These may here receive brief mention. The first to be considered is one by Batten. His observations pertain largely to muscle-spindles found in man. The material was hardened in Müller's and Marchi's fluids and stained in hematoxylin and eosin and after Pal's and Sihler's methods. He has this to say of the ending of the spindle-nerves :

"The nerve-fibers terminate in various ways ; as a rule, the large fiber which enters the equatorial region passes directly to the muscle-fiber, and seems to lose itself in the nuclei of the muscle-fiber above described ; some fine fibers pass between the muscle-fibers and terminate in such an organ as is figured in (Fig. 7) ; others seem to have a spiral form. Others again form a fine plexus beneath or in the sheath of the spindle." In Fig. 7, which is reproduced from a photograph, the ending is only imperfectly shown, it would seem however to resemble the flower-like ending of Ruffini. From this figure, as also from Batten's description of the nerve-endings, we are led to believe that the endings seen by him show only partially stained nerve-endings, the methods used by him being therefore not so reliable as the gold chloride method, much less the methylene-blue method for staining the ultimate endings of the spindle-nerves.

The latter part of Batten's paper deals with the behavior of the muscle-spindle in certain pathological conditions : infantile paralysis, tabes, myopathy (Leyden's form), progressive muscular atrophy, peripheral neurites, injury to the brachial plexus, after section of the sciatic in cats.

Batten shows that "in infantile paralysis the spindle remains absolutely normal, although the surrounding tissue undergoes complete atrophy. In tabes, he shows that certain changes take place in the termination of the nerve, the general structure of the spindle remaining normal. In progressive muscular atrophy the spindle remains unaltered, and the same is probably true with regard to peripheral neurites. Section or

atrophy of the nerve trunk leads to atrophy of the muscle-fibers within the spindle, though it is probable that it takes a considerable length of time for changes to take place in the muscle-fiber within the spindle."

Spiller describes the muscle-spindle in a case of intense muscular dystrophy. The muscle-spindles were normal, also medullated "intra-muscular nerves." He gives no observations on the ending of the spindle-nerves.

Horsley, in a brief note accompanied with photographs, summarizes observations made on trans-sections of *gastrocnemii* and *solei* of dogs and cats in which the sciatics were divided at periods varying from 3 days to 1 year before the animal was killed.

Horsely shows that although the muscle-spindle seems to undergo an apparent shrinkage from about the 17th day after the section of the nerve, this shrinkage is parallel to the general shrinkage which the atrophy of the muscle gradually undergoes as a whole, the intrafusal fibers being apparently unaltered in character.

In a case of pseudo-hypertrophic paralysis, in which the muscle-spindles were examined by Grünbaum, he finds "the muscle-spindles were for the most part unaffected, but in a few there was a diminution in size of an intrafusal fiber with a deposit of hyaline material around."

We wish finally to refer briefly, to that portion of Ruffini's recent note on the sensory endings in striated muscle, in which he summarizes his observations on the spindle-nerves. Ruffini has studied more particularly the muscle-spindles in the cat, and describes these three kinds of endings of the spindle-nerves:—primary, secondary, and plate-like.

*Primary endings.* The large nerve-fiber going to the spindle almost always divides into two or more secondary branches, each of which divides into tertiary branches after having passed through the capsule; each of these ends on the intrafusal muscle fiber. These tertiary branches lose their sheath of myelin, become broad, flat and ribbon like, and are either spirally wound about an intrafusal fiber or run along one side of it

as a longitudinal band from which, from point to point and at varying intervals, 'troop-like terminal expansions' clasp the entire circumference of the fiber. To these the name of "annulo-spiral ribbon endings" is given.

*Secondary form of ending.* The parent nerve also divides into secondary branches but usually only after having penetrated the spindle. "The secondary branches soon break up into a number of varicose axis-cylinders, united by very delicate and short filaments. The varicosity of the nerve-fibrils is of various kinds, rounded, bifid, triangular, leaflet-like." This ending is called the "flower-wreath ending."

*Plate-like ending.* These vary greatly in size. Some are smaller than the end-plates, some equal to them in size some much larger; the last named are the most usual. They differ from the ordinary end-plate. "The terminal expansion of these plate-endings are attached to short and extremely delicate filaments, so that they form, as it were, chaplets, in which rounded axis-cylinders and cross-pieces of the finest delicacy succeed each other in turn."

These three forms of endings are not found in every spindle. Ruffini thus distinguishes three forms of spindles:

1. Spindles with complex nerve ending;
2. Spindles with simpler nerve ending;
3. Spindles with simplest nerve ending.

As to the first four of the five papers here briefly reviewed we wish to add only a few words of comment:

1. From the observations in pathological cases referred to in the above review, it would seem safe to venture the statement, that in such cases where the motor nerves or muscle fibers are primarily affected, the muscle-spindle is not altered in appearance so far as may be determined with the more ordinary histological methods.

2. Strangely as it may seem, after section of the nerve going to the muscle, the muscle-spindle does not materially alter its structural appearances, even after a considerable period of time has elapsed since the section of the nerve. This seems

the more inexplicable, since, as we have shown, the intrafusal fibers are supplied with a motorial ending. We have at the present time no observations to offer in explanation of this fact. So far as we are aware, no concerted effort has been made to ascertain the behavior of the spindle-nerves, and we refer here more especially to the ultimate ending of these nerves, after nerve-sections. This we hope to do in the near future, also to ascertain as to whether so complicated a nerve-ending is capable of regeneration.

As to the account of the ultimate endings of the spindle-nerves given by Ruffini in the note from which we have quoted, we would say,—that, so far as we can determine from the brief account given by him, he has not materially added to his former, and more fully reported observations, which in the preceding pages we have quoted; and further, that we believe our figures will show the various forms of ending mentioned by him, with the exception perhaps of the plate-like endings. Concerning these it is rather difficult, owing to the meager account given, to form a definite idea as to the kind of ending Ruffini had in mind when formulating his description.

A division of the muscle-spindles into the three forms given by Ruffini seems to us somewhat arbitrary. The configurations of the ultimate endings differ, yet these differences appear in every well-stained spindle. A division into simple and complex, or perhaps better compound, spindles—simple, with only one area of nerve distribution, compound, with two or more such areas—seems to us more justifiable.



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#### DESCRIPTION OF FIGURES.

All figures were drawn under the 1-12 in. oil immersion, and No. I eyepiece (Leitz) with the aid of the camera lucida, giving them a magnification of about 900.

The colored figures are from tissues injected with methylene blue, fixed in ammonium molybdate, sectioned in paraffin and double stained in alum carmine or alum cochineal and mounted in balsam. The other figures are from methylene blue preparations, fixed in ammonium picrate, teased, cleared and mounted in a glycerine-picrate-solution. The latter figures are reduced as will be indicated later.

#### PLATE XIV. MOTOR NERVE-ENDINGS.

*Figs. 1 to 11.* Motor nerve ending in voluntary muscle of rabbit. Axis cylinder and ending stained blue; other structures, red.

*s.*—sarcolemma.

*n. l.*—neurolemma.

*t. n.*—telolemma nuclei.

*Figs. 1 to 5.* Surface view of muscle fiber and nerve ending.

*Figs. 6 to 8.* Longitudinal section of muscle fiber and motor ending.

*Figs. 9 to 11.* Cross-section of muscle fiber and nerve ending.

*Figs. 12 to 14.* Nerve ending in amphibian muscle—frog.

*Fig. 12.* Surface view of muscle fiber and nerve ending.

*Figs. 13 to 14.* Cross section of muscle fiber of frog and hypolemmal nerve fibers.

The lettering is here the same as in the previous figures.

*Figs. 15 to 21.* Ending of nerve fibers on cardiac muscle of the auricle of the cat's heart.

*Figs. 15 to 20.* Surface view of cardiac muscle cells with nerve endings of varying degrees of complexity.

*Fig. 21.* Cross section cardiac muscle cell with nerve ending.

*Figs. 22 to 24.* Ending of nerves in involuntary, smooth muscle from muscular wall of the intestine of a cat.

*Figs. 22 to 23.* Longitudinal section.

*a.*—axis cylinder terminating.

*b.*—termination.

*n*—nucleus of the cell.

*Fig. 24.* Cross section of involuntary muscle cell through the point where nerve fibril terminates.

#### PLATE XV. NERVE-ENDING IN MUSCLE-SPINDLES.

*c.*—capsule.

*a. s.*—axial sheath.

*c. n.*—connective tissue sheath, surrounding each intrafusal fiber; only here and there designated.

*i. f.*—intrafusal fiber.

*p. a. s.*—periaxial space.

*s. n.*—medullated spindle-nerve.

*H. S.*—Henle's sheath.

*s. m.*—striated muscle fiber from muscle, given to show the relative size of intrafusal and the other striated muscle fibers.

*Sy. n.*—sympathetic nerve fiber—vaso-motor fiber.

*bl. v.*—blood vessel.

Nerve fibers and endings blue, all other structures red.

*Figs. 25 to 27.* Muscle-spindles of amphibia.

*Fig. 25.* Longitudinal section of the distal portion of the muscle-spindle.

*Fig. 26.* Cross section of a muscle-spindle at the place of entrance of a spindle-nerve.

*Fig. 27.* Cross section of the distal portion of a muscle-spindle.

*Figs. 28 to 30.* Muscle-spindles of tortoise.

*Fig. 28.* Longitudinal section through equatorial region, showing entrance of spindle-nerve.

*Fig. 29.* Cross section of distal portion of muscle-spindle.

*Fig. 30.* Cross section of muscle-spindle through place of entrance of spindle-nerves.

*Figs. 31, 32.* Muscle-spindle of a bird.

*Fig. 31.* Longitudinal section of muscle-spindle of a dove, showing the ending of one of non-medullated terminal branches (*a*) of a spindle-nerve.

*Fig. 32.* Cross section of muscle-spindle of a dove.

#### PLATE XVI. MUSCLE-SPINDLE OF MAMMALIA.

Lettering the same as on plate XV.

*Fig. 33.* Longitudinal section of compound muscle-spindle from the intrinsic plantar muscle of the rabbit.

*Fig. 34.* Cross section of muscle from the intrinsic plantar muscle of a cat.

*Fig. 35.* The same.

#### PLATE XVII.

*Fig. 36.* Muscle-spindles from cutaneous pectoris muscle of frog. Reduced to one half.

*Fig. 37.* Muscle-spindle from back muscles of the snake. Reduced to one half.

*m. e.*—motorial ending; *m. e. (a)* is under the fiber and probably the ending is on another fiber.

*Fig. 38.* Muscle-spindle from intrinsic plantar muscles of a dog. Reduced to one half.

#### PLATE XVIII.

*Fig. 39.* Compound muscle-spindle from the intrinsic plantar muscles of a dog, showing three areas of nerve distribution.

*Sy. n.*—Sympathetic nerve fibers—vaso-motor fibers.

*m. e.*—motorial endings.

Reduced three times.

## EDITORIAL ANNOUNCEMENT.

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The present issue closes the seventh volume of the JOURNAL OF COMPARATIVE NEUROLOGY. Seven years ago the first number appeared with neither financial support nor influential collaboration and, notwithstanding manifest imperfections and limitations, it has steadily kept in view its initial purpose to promote the investigation of the nervous system by the broadest possible application of the comparative method. We take this opportunity to thank those who from the start have offered encouragement and practical aid. The JOURNAL has never been the organ of a party or institution or a special pleader or propagandist and will continue to maintain an unprejudiced attitude toward all worthy efforts, particularly welcoming the results of independent research.

The editors have pleasure in announcing that, beginning with the first number of volume eight, greatly enlarged facilities will be afforded by the addition of a number of collaborators, each of whom has attained a position of eminence as an investigator in the department which he represents. It is not as yet possible to announce the names of all the collaborators, but the following may be mentioned at this time :

Professor Ludwig Edinger, *Frankfurt, a-M.*, Collaborator for Germany.

G. Carl Huber, M.D., *Assistant Professor of Histology and Embryology in the University of Michigan*; The sympathetic system and the peripheral nervous system.

B. F. Kingsbury, Ph.D., *Instructor in Microscopy, Histology and Embryology, Cornell University and The New York State Veterinary College*; Morphology of the lower vertebrates (Ichthyopsida).

Adolf Meyer, M.D., *Docent in Psychiatry, Clark University, and Assistant Physician to the Worcester Lunatic Hospital*; Human neurology.

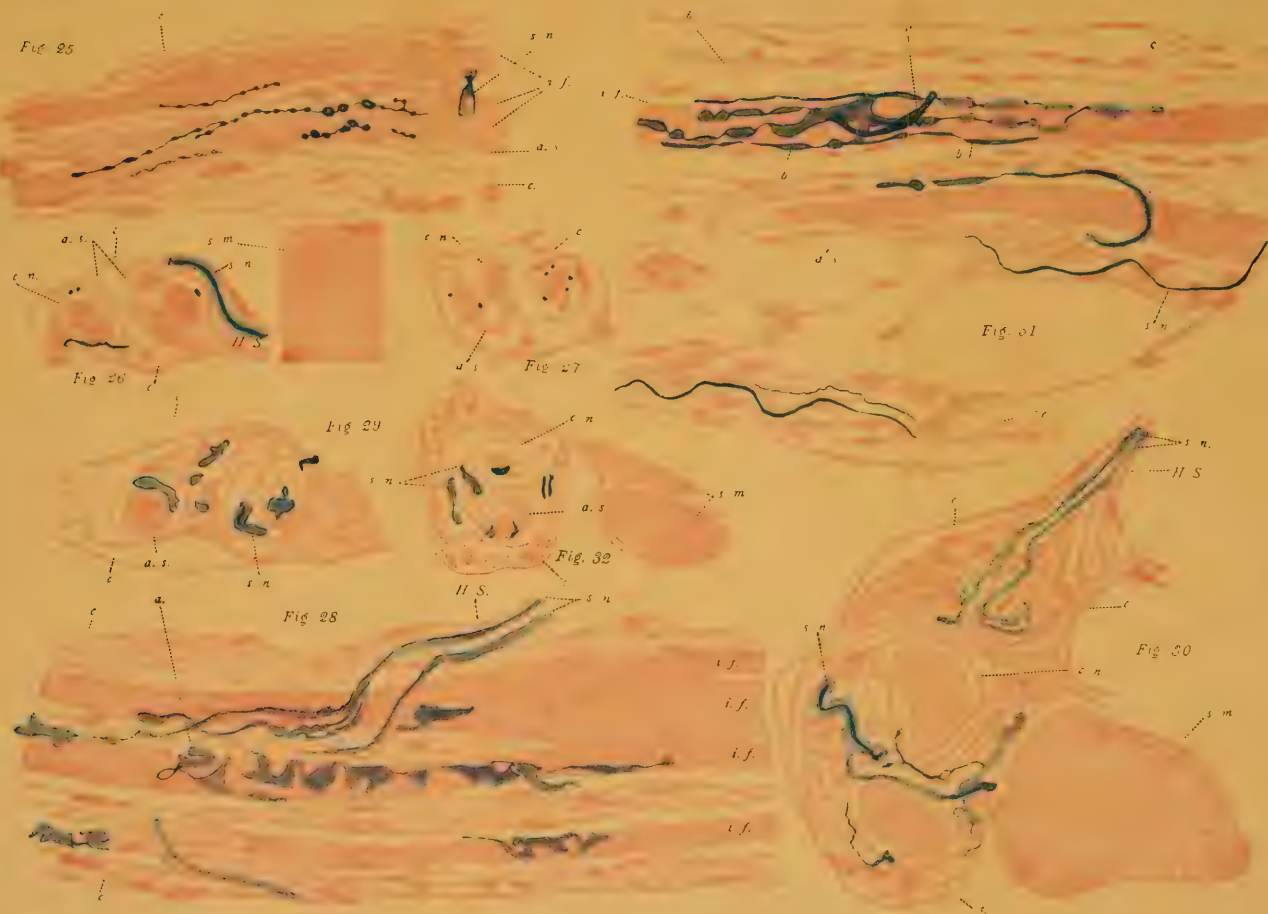


As heretofore, the JOURNAL will be international in scope, and no pains will be spared to make it reflect the latest and best developments in neurological research. It is hoped to increase its educational value by affording at frequent intervals comprehensive critical and historical reviews of particular topics, designed in part to keep the specialist in touch with the whole field of the literature, and in part adapted to the needs of the non-technical reader. Due attention will be given to the psychological bearing of neurological discoveries, as well as to the data of comparative psychology. There is no other periodical in any language which occupies this field, which is, however, cultivated by a large proportion of our most able morphologists and physiologists and which has important applications in the great departments of human pathology, psychology, pedagogy, etc. We therefore appeal with confidence to all those interested in progress along these lines for cordial support. The editorial enlargement now provided for will involve an increase not only in number of pages, but also in the cost of the illustrations furnished. The extent of such improvement, however, must depend, largely, upon the liberality with which the presumptive constituency of the JOURNAL responds to our efforts, since the JOURNAL has no permanent endowment and the few who are now meeting the chief expenses of publication can hardly be called upon for larger contributions.

While President Herrick of the University of New Mexico continues as editor, the active editorial management will remain, as heretofore, with Dr. Oliver S. Strong of Columbia University and Professor C. Judson Herrick of Denison University, the latter being also the publisher. Contributions and papers for review may be sent to any of the editors, but correspondence relating to the details of publication and all business communications should be addressed to C. Judson Herrick, at the publication office, Denison University, Granville, Ohio, U. S. A.

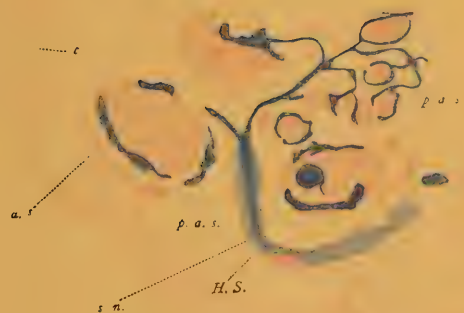
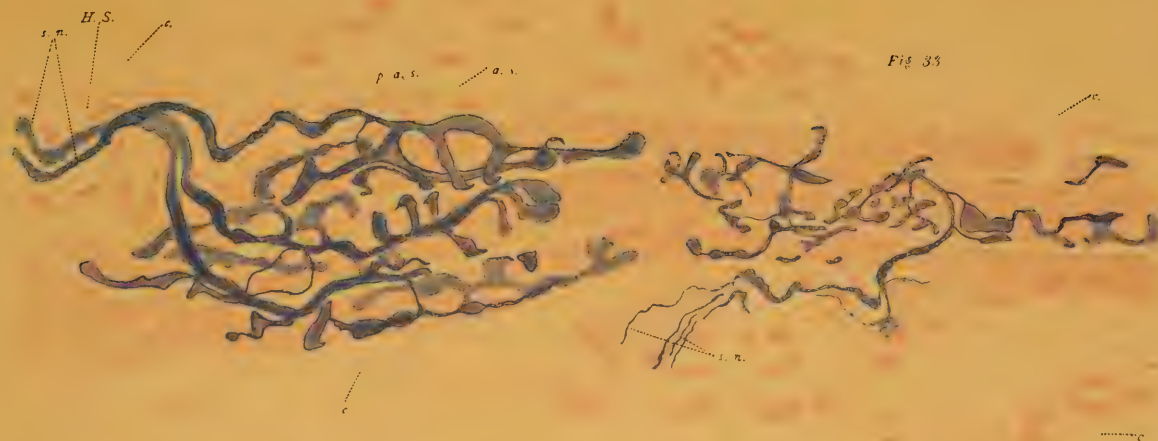








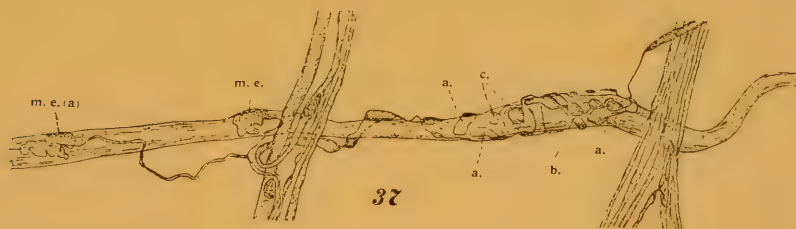








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## LITERARY NOTICES.

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### **Edinger's Lectures—Fifth Edition.<sup>1</sup>**

It is difficult to speak in measured terms of the new edition of this highly appreciated work. Nothing less than delight expresses ones feelings in turning the well-printed, fully illustrated pages. Delight that the essentials of descriptive brain-anatomy have been so clearly and adequately presented, delight that the results of modern histology have been appreciatively and conservatively employed and, more and better than all, that we now have an approach toward an outline of comparative neurology in convenient and orderly form. No one can rise from even a casual perusal of this work without having grasped the fact that the comparative method lies at the basis of all true comprehension of the nervous system. While judicious and conservative, the work before us is progressive and comes fresh from the laboratory with evidence of research on every page. Here for the first time we have the attempt to present a picture of the vertebrate central organs as a consistent whole and the result inspires confidence that the discrepancies between the various groups will disappear when sufficiently investigated. From 220 pp. the volume has grown to 386 and the greater part of the additional matter is comparative. While the author has based his descriptions upon original work to an extent quite beyond all expectation, he nevertheless has not ignored the work of those who preceded him.

The first part contains, beside the historical introduction of the old edition, a discussion of the neurocyte and cellular histology and a very useful summary of the elementary facts of cellular physiology. The fourth lecture is devoted to embryology and is perhaps less satisfactory than most of the other sections by reason of its brevity and the consequent omissions. Then follow nine lectures (all new) devoted to the comparative anatomy of the brain and cord. The illustrations are nearly all new, though many are based on the author's published studies. The treatment of the reptile brain is especially full and sat-

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<sup>1</sup> Vorlesungen über den Bau der Nervösen Centralorgane des Menschen und der Thiere. *F. C. W. Vogel, Leipzig, 1896.*



tisfactory. One matter calls for especial notice. The author has endeavored to apply topographical terminology, especially in the naming of tracts. Thus we have *tractus tegmento-cerebellaris*, *tractus tecto-bulbaris*, employing a principle long in vogue in the nomenclature of muscles. Of course, in many cases the ultimate origin and destination of a tract remain in doubt and in some instances a name can only be tentative. On the other hand the convenience of employing a name which is also descriptive is obvious. There will be a difference of opinion respecting many points in the terminology used but, without being in any sense radical, the tendency of the usage is distinctly toward consistency. We regret, for example, that the term sulcus and fissura are both employed upon the cerebrum and that folium is not given a generic instead of specific application in the cerebellum. We object to the use of the term valvula for the volvula cerebelli in fishes and of torus semicircularis for colliculus. There seems at times to be ambiguity in the use of the terms lobus olfactorius, area olfactoria, spatium olfactorium parolfactorius and lobus pyriiformis. We are not satisfied that the homology of the axial lobe of lower vertebrates with the striatum is sufficiently clear to apply the latter term in those groups, and there are numerous moot points which only the combined efforts of many investigators can settle; but this fact does not detract from our appreciation of the value of this first successful attempt to lay the foundation for a homogeneous science of neurology.

The third part, while less altered than the other chapters, is largely rewritten and is supplied with new illustrations. The portion relating to the development of the olfactory organs and their function is familiar to our readers but is expressed with more conservatism than in earlier papers. There are several points in the earlier edition from which the author retreats or withholds judgment. We agree with him that there is insufficient proof that the entire gyrus fornicatus has an olfactory function. As to the homology of the psalterium with both cephalic and caudal mantle-commissures we await farther developments with interest.

Some readers will miss the final paragraph on methods from the present edition but it is evident that the book has nearly reached the upper limits for a one-volume text-book and the modern histological technique can hardly be satisfactorily treated in a chapter. Much as we dislike the term "epoch-making" the present edition certainly does mark the beginning of the comparative epoch in neurology.

C. L. H.

**Micro-Chemical Alterations in Nerve Cells.<sup>1</sup>**

This paper undertakes the study of functional changes in nerve cells from the stand point of micro-chemical analysis of the intracellular metabolic products and their qualitative and quantitative alterations.

The research was conducted upon the spinal ganglion cells of the rabbit, the seventh lumbar segment being especially chosen because it receives the greater part of the fibers from the sciatic nerve. The difficulty was to secure for a sufficient length of time absolute rest of the nervous elements—thus preventing the formation of new metabolic products—and at the same time to keep the cells alive, so that they might eliminate those produced. To this end the sciatic nerve was resected and the animal kept alive two days thereafter. Fatigue on the other hand was produced by exciting the sciatic nerve with a Du Bois-Reymond apparatus, the excitation lasting from 30 minutes to 8 hours. The ganglia were then as quickly as possible treated with the fixing reagent, and for this purpose Hermann's fluid was selected as it best preserves both the granules and the cytoplasmic structures. The sections were stained variously, chiefly in acid fuchsin decolorized with picric acid and methyl green.

The author, following Lugaro, agrees with Flemming in finding the cytoplasmic structure distinctly filar, the threads being brought out clearly by the methyl green and lying among rather large masses of dense protoplasm which appear homogeneous and react to the stain like the threads. Besides these masses, there were sparse and very minute granules which resist the action of the decolorizer and therefore appear red. These fuchsinophile granules were the objects of special study. In normal cells, i. e. those removed from the body by vivisection, they occur in the clear interfilar spaces and are occasionally elongated. They occur in less abundance in the vacuolar spaces of the nucleus.

After resection of the sciatic nerve and consequent rest, i. e. after long freedom from stimuli, the size of the fuchsinophile granules was reduced ; in some elements they could not be found at all.

After excitation of the sciatic nerve for half an hour there was a conspicuous increase of the granules, as compared with the ganglia removed by vivisection. The nucleus is without granules. If the excitation is prolonged for two hours, the number of the granules greatly

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<sup>1</sup> LEVI, G. Contributo alla fisiologia della cellula nervosa. *Rivista di Patol. Nervosa e Mentale*, I, 5, May, 1896.

increases. Cells destitute of them are rare. The granules may be very small and exceedingly numerous or larger than normal and fewer, sometimes elongated. If the excitation is continued for 8 hours, the result does not differ quantitatively from the last case, but some granules appear dark brown. At the margin of the cell were groups of large granules colored dark yellow.

These experiments are certainly suggestive, but the methods employed seem too unreliable to yield conclusive results. In particular, those used to secure both rest and fatigue seem open to the objection that they depart too far from normal physiological processes and may induce structural changes of many other kinds than the simple effects desired.

C. J. H.

### Halleck's Education of the Central Nervous System.<sup>1</sup>

Mr. Halleck argues that education involves structural changes in the nervous system and that a knowledge of these changes will conduce to better educational methods. From the title we should expect a book treating primarily of the nervous system and its developmental hygiene, and such it nominally is. Really, however, the book is written from the pedagogical and psychological standpoint throughout. The author evidently has not that first-hand knowledge of the nervous system which would enable him to speak with authority in this department; yet he has made good use of his text-books and the references to the neural processes involved in mental life add force and illustration. They can hardly be said to do more.

In a work devoted to the Education of the Central Nervous System in which no knowledge of brain structure or function is presupposed we should have expected a more full treatment of these topics than can be compassed in 27 pages. Yet one thoroughly conversant with the recent periodical literature would have made up even so brief an account quite differently. There is no suggestion of the modern ideas of nervous connection and transmission based upon the so-called neuron theory nor of the details of the fiber connections of the cortex about which so much positive information has been gained within the last few years. Nor is the little that is given always exact. For example, the following on page 29 could never have been written by one familiar with the recent controversies between Professors Munk and Goltz,—“When stimuli cause the rest of the nervous system to

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<sup>1</sup> The Education of the Central Nervous System. By REUBEN POST HALLECK, M. A. New York: The Macmillan Co., 1896.



act after the cerebral hemispheres have been removed, there is no dispute over the fact that such movements are due to the workings of a nervous machine and nothing more."

We heartily commend the author's emphasis upon the necessity for an out-of-door life and a symmetrical training of all the senses if we would secure the highest educational results; but Mr. Halleck's system, like his book, is too ill-balanced to be safely followed.

C. J. H.

### The Morphology of the Optic Nerve.

The fact that the optic "nerve" is not a nerve at all in the strict sense of the term, but an integral part of the central nervous system is of course now all but universally recognized. Yet its position is in many respects unique and the problems connected with its morphology and evolution are by no means all happily settled. Thanks to the labors of W. Müller, Kölliker, Keibel, Cajal and Frioriep, among others, we may now consider it definitely established that the major part of the fibers of the optic nerve arise in the ganglion cells of the retina and grow centrally to terminate in arborizations in the tectum, while there is a reasonable probability that a smaller number of fibers arise in the tectum and pursue the opposite course. Yet one of the more recent contributors to this question<sup>1</sup> asserts that in the frog the fibers in growing from the retina to the optic tectum pass, not through the optic stalk, but outside of it. "The optic nerve is developed independently of the optic stalk, the nerve fibres lying along the posterior border of the stalk, and at first entirely outside it; but on the breaking down of the stalk, some of the nerve fibres grow in between the cells." This is equivalent to saying that a tract of fibers in passing from one part of the central nervous system to another takes a path which for a part of its course lies entirely outside of the system—certainly an improbable condition. In order to test the matter Dr. Arthur Robinson has followed the development of the optic nerve in a number of representative mammals.<sup>2</sup> In brief, he confirms the results of the first mentioned authors that the nerve fibers grow inside of the optic stalk and among the cells which constitute its wall. He

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<sup>1</sup> ASHETON, R. On the Development of the Optic Nerve of Vertebrates and the Choroidal Fissure of Embryonic Life. *Quart. Jour. Micr. Sci.*, August 1892.

<sup>2</sup> ROBINSON, ARTHUR. On the Formation and Structure of the Optic Nerve and its Relation to the Optic Stalk. *Jour. of Anat. and Physiol.*, XXX, N. S. X, 3, April, 1896.



says, "In mammals the optic stalk becomes converted into the optic nerve by the transformation of its protoplasmic substance into retiform sustentacular tissue, and by the passage of nerve fibres through its walls, the nerve fibers being protected and supported by the external limiting membrane of the stalk, and by the reticular framework formed by the modification of its walls, the transformation from the stalk to the nerve being associated with the disappearance of the cavity of the stalk."

In further discussing the relation of the retina and optic nerve to the brain, Dr. Robinson calls attention to the differences between the retina and the other sense organs. The fact that the retina is an evagination from the brain he regards as involving the absence of both peripheral nerve and ganglion, external stimuli impinging directly upon the central organs; and from the fact that the optic evagination takes place from the ventral part of the primary vesicle he is inclined to look upon the retina as a modified basal ganglion and the optic nerve as an association bundle bringing it into relation with other parts of the brain. The facts, however, are capable of quite a different interpretation in the light of the most recent researches. It will be remembered that Eycleshymer and Locy have described protons of the optic vesicles on the cephalic plate even before its invagination to form the neural tube and that Locy recognizes behind these vesicles other accessory vesicles, one pair of which he regards as the protons of the epiphysis. The elements of the retina therefore can be traced directly back to definite areas of ectoderm, like the cranial ganglia in general and they cannot be compared with basal ganglia. It has been suggested that we go a step farther and compare the cells of the ganglionic layer of the retina with the cells of the cranial ganglia and the fibers of the optic nerve with root fibers. Thus the retina, though a part of the brain, may at the same time contain structures which are ordinarily found in peripheral ganglia.

Final judgment on these questions is probably at present premature, but an interpretation along these lines seems to the writer to be better in accord with the existing evidence than to regard the retina as a basal ganglion.

However clearly the facts of development may point to the community of origin of the optic apparatus and the other parts of the brain, there still remain in the adult structures of the lower vertebrates especially many points difficult of interpretation. Several comparative studies of the optic nerves of vertebrates have been made. The

most recent is that of Studnicka<sup>1</sup> who has devoted himself especially to filling the gaps in our knowledge of the optic nerve in the Ichthyopsida and Reptilia.

Even the most aberrant forms can clearly be derived from the embryonic tubular optic stalk. In Petromyzon the lumen of the stalk soon disappears, but its cells, or their descendants, persist throughout life as an axial core of glia cells in the nerve. In Protopterus there is also an axial strand, but the cells are few and scattered and the nerve is more or less completely separated into strands by connective tissue septa entering from the periphery. In Ceratodus and Lepidosiren this separation has been carried further until we have very numerous distinct strands each with an axial core of cells. The simplest condition is found in Necturus, where the lumen persists throughout life. In other Amphibia there is either an axial mass of glia cells or many such series scattered through the cross section of the nerve, and this is the condition in the higher animals in general.

In the fishes, however, the deviations from the original condition are very great. Among the selachians, Chimaera has a simple cylindrical nerve with the glia cells scattered uniformly through it and with no connective tissue septa. In the sharks, however, such septa may be very highly developed, even to the division of the nerve into very numerous small strands with septa between them. This destroys the earlier generalization of Deyl<sup>2</sup> that, as we pass from low to high in the vertebrate series the amount of connective tissue in the opticus progressively increases.

Polypterus resembles the Selachii more closely than the other ganoids. Acipenser and Polyodon show the band-form which is so characteristic of teleosts, while Lepidosteus carries this type to its extreme, the band being very wide and plaited several times. The latter form is very common among teleosts. Studnicka differs from Deyl in regarding it as derived by the folding of a ribbon-shaped nerve, rather than as derived from a cylindrical nerve by the intrusion of connective tissue septa. In Hippocampus the whole nerve is broken up into a number of separate strands, but these are shown by their arrangement to be derived from a plicated band by the interposition of complete septa. Deyl attempts to deduce certain phylogenetic considerations from his study of the optic nerves, but Studnicka

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<sup>1</sup> Untersuchungen über den Bau des Sehnerven der Wirbeltiere. *Jenaische Zeits.*, XXXI.

<sup>2</sup> Zur vergleichenden Anatomie des Sehnerven. *Prag*, 1895.

shows that this character is too variable and too liable to convergence to have any very wide application in this direction.

The remarkable forms assumed by the optic nerves of fishes are striking illustrations of the amount of variation possible in a very simple structure under varying conditions, the decisive factor in this case being probably the necessity for the proper nourishment of the nerve in large-eyed species.

Another interesting point brought out in this connection is the fact that the parietal nerve in *Ammocætes* develops the same as the optic, as a tubular outgrowth into which fibers grow from the retina and the original cells of the tube are, as before, crowded into an axial strand and transformed into glia cells. It is very interesting that a nerve so little differentiated as the nerve of the pineal organ can be divided into several parallel strands in the course of its development.

C. J. H.

#### The Cerebral Fissures of the Lemurs.<sup>1</sup>

Professor Ziehen continues his studies of the surface anatomy of the cerebrum. Having already devoted considerable attention to comparisons between the fissures of the primates and various carnivora and allied types, the chief interest in this study centres about the question of the relations of the prosimian to these two types of fissures. The result of a detailed comparison is the conclusion that while the lemurine fissuration is directly comparable to the carnivore type (this is illustrated in a comparative table), yet it is nearer to that of the primates. In fact, the prosimian type is to be regarded as the prototype or fore-runner of the primate, but not as an intermediate stage between the latter and the carnivore. The carnivora and the primates exhibit a common fissural plan, which has, however, been independently elaborated in the two cases. Within the Prosimia, however, we find no evidence of more than one phylum. On the other hand the comparative anatomy of the cerebral surface shows a unity of structure which cannot be explained by convergence. We must refer the reader to the figures and tables of the author for the data on which these conclusions are based.

C. J. H.

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<sup>1</sup> ZIEHEN, TH. Ueber die Grosshirnforschung der Halbaffen und die Deutung einiger Furchungen des Menschlichen Gehirns. *Archiv f. Psychiatrie*, XXVIII, 3.

## LITERARY NOTICES.

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### Development of the Fifth Nerve in Man.<sup>1</sup>

This research was conducted upon the series of human embryos belonging to Professor His and is the first complete account of the development of the fifth nerve of man.

Professor His has described <sup>2</sup> the early development of the fifth nerve up to the time when the three great divisions are separated. Beginning at this stage with an embryo of four weeks, Dr. Dixon has followed the subsequent development of the rami and their ganglia. The observations on human embryos were controlled with rat embryos of various ages and they were found to correspond in every important particular. Transparent models of the various stages were constructed by transferring camera drawings of the sections to glass plates.

*Ophthalmic Division.*—At the beginning of the sixth week (13.6 mm.) nasal and frontal rami have developed and in connection with the latter the ciliary ganglion. The nerve passes through the ganglion as a solid bundle, no fibers wandering out among the ganglion cells. The fourth nerve communicates with the frontal proximally of the ciliary ganglion and the remainder of its fibers at this stage enter the ciliary ganglion and terminate in it. The third nerve at this stage does not enter into relation in any way with either the ciliary ganglion or the fifth nerve. The fourth nerve has a broad communication with the frontal at seven weeks also. At the eighth week the third nerve sends a branch to the ciliary ganglion, the latter sends twigs to the eyeball, and the nerves of the orbit have practically the disposition that obtains in the adult. The nasal nerve runs through the ciliary ganglion, while the frontal has no connection with it. The ganglion found in the sixth week in connection with the fourth and frontal

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<sup>1</sup> DIXON, A. FRANCIS. On the Development of the Branches of the Fifth Cranial Nerve in Man. *Trans. Roy. Dublin Society*, Ser. 2, VI, May, 1896, pp. 19-76.

<sup>2</sup> *Abhandl. Kgl. Sächs. Ges. d. Wiss.* 1888, XIV, p. 341.



nerves seems therefore to have migrated to the third and nasal nerves.

The interesting problems connected with the ciliary ganglion are discussed quite fully. It is not the same as the mesocephalic ganglion of Beard in the Elasmobranchs. The nasal nerve of man is identified with the ophthalmicus profundus of Elasmobranchs, and the frontal with the ophthalmicus superficialis trigemini. The author is inclined to regard the ophthalmic, or mesocephalic, ganglion as fused with the Gasserian in man and the rat, for in both of these cases the nasal and frontal nerves from the first arise as branches of the Gasserian ganglion. The ciliary in man is, therefore, a purely sympathetic ganglion.

It has of late been stated independently by several writers that the third and fourth nerves differ from other motor nerves in that they grow from peripheral ganglia into the brain. That there is a transient ganglion and a centripetal growth in each case seems pretty well established, but if Dixon's explanation holds, the case is by no means as anomalous as might at first appear. He assumes, following Miss Platt, that in each case we have a "cellular nerve" or proton developed from the ganglion to the brain, into which the fibers subsequently grow centrifugally from the brain. What the significance of this transient cellular proton may be is not made plain.

*Superior Maxillary Division.*—This nerve is at first unbranched and is not connected with any ganglion except the Gasserian, from which it grows.

*Inferior Maxillary Division.*—This too is unbranched at first and the inferior dental nerve is to be looked upon as the direct continuation of the first formed inferior maxillary division of the fifth nerve. All the important branches of the inferior maxillary nerve are represented in the embryo at the beginning of the sixth week. At this time the two accessory ganglia of the inferior maxillary nerve appear nearly simultaneously, and no proof was found that their cells are derived directly from the cells of the Gasserian ganglion. Their development indicates that they must be regarded as typical sympathetic ganglia and in no sense compared to spinal ganglia.

The development of the connections of the trigeminal with the seventh and ninth nerves is of great interest. At the fifth week the chorda tympani nerve does not join the lingual, but is connected only with the seventh nerve. In this embryo also the vidian nerve does not yet communicate with the ganglion of Meckel or superior maxillary nerve. Both of these nerves are therefore branches of the sev-

enth nerve and are doubtless derived from the geniculate ganglion. The nerve of Jacobson at the same age is seen to be an outgrowth of the petrous ganglion of the ninth nerve and is not yet connected with the trigeminal. In all of these points the rat embryos agree exactly. The author adds, "The fact that these connecting nerves are not branches of the trigeminal, but of the facial and glossopharyngeal, renders it improbable that through them taste impressions are transmitted to the fifth nerve, and so to the brain." "Embryologically, the nerve supply of the organs of taste appears to be derived from the facial and glossopharyngeal nerves alone, since the lingual admittedly in itself contains no taste fibers." This result, though contradicted by considerable clinical experience,<sup>1</sup> yet conforms with recent comparative work, especially that of Strong in Amphibia and the writer in fishes, where it has been shown that all organs of taste are supplied by the fasciculus communis component of the VII and IX+X nerves, the fifth taking no part in their innervation.

C. J. H.

#### Degenerative Changes in the Brain of the Non-insane.<sup>2</sup>

The paper before us raises an interesting question. It must, of course, be admitted that in the brain cells are constantly wearing out and being replaced by others. It might be expected that suitable histological methods would reveal in the average brain such degenerating cells along with such as are normally functional. This a very casual study of the brain will substantiate. The author has undertaken to investigate the nature of such degenerative changes in the non-insane, employing only the freezing method of Bevan Lewis. While hardly the most desirable method for such a study it was selected for practical reasons.

In comparing a series of fifty brains of non-insane with an equal number of asylum patients he reports no greater frequency of patho-

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<sup>1</sup> Compare especially ADOLPH SCHMIDT. Ein Fall vollständiger isolirter Trigeminuslähmung nebst Bemerkungen über den Verlauf der Geschmacksfasern der Chorda tympani und über trophische Störungen. *Dtsch. Z. f. Nervenheilk.*, VI, 5-6, 1895, pp. 438-457.

The case here cited conclusively proves that sensations of taste are transmitted from the anterior two thirds of the tongue by means of the chorda tympani. The clinical evidence presented to prove that these chorda fibers enter the brain through the fifth nerve instead of the seventh seems to us by no means so conclusive.

<sup>2</sup> HUTCHINSON, ROBERT. *Edinb. Hospt. Rep.*, Vol. IV.

logical change in one set than the other (always excluding cases of general paralysis where the changes are always conspicuous). Increased pigmentation with age was apparently allowed for and the pseudo-vacuolation often mistaken for a pathological state is noted. Changes in the connective elements and blood-vessels are less frequent. The author concludes that the lesions of most insanities differ in degree more than in kind from the degenerations of growth.

C. L. H.

### Division of Nerve Cells.

Rohde describes <sup>1</sup> the processes of division of functional nerve cells in the gasteropods. Leaving out of account his theories of the participation of the neuroglia in the formation of the cell bodies, his three types of division are as follows: (1) one or more nucleoli wander out of the nucleus and, carrying a part of the cytoplasm with them, are extruded to form new cells, the parent cell remaining unaltered; (2) daughter nuclei are formed by budding everywhere throughout the parent cell which finally fragments and is consumed by the process; (3) the nucleus breaks up by direct nuclear fragmentation, not by budding, into a large number of smaller nuclei each like the parent. Though the author's statement, "In the literature there is no account of a multiplication of ganglion cells" is not strictly true; yet it is true that the few cases known, including that of Ayers published since this article, present nothing comparable to the processes here described. It has its parallel only in the endogenous nuclear division of certain of the Protozoa.

C. J. H.

### Monatsschrift fuer Psychiatrie und Neurologie.

Professors Wernicke and Ziehen in projecting this new monthly, which begins with the year, have in the numbers already out fully answered any question which may have arisen as to the need of a new periodical. The original articles are not only of solid worth but represent the leading institutions of Europe from London to Rome. In the brief "Tagesfragen" which introduces the first number some of the signs of the times are briefly sketched. Notable among these is the tendency to systematize, to schematize, our knowledge. This is indeed a factor of our present and future progress of no mean impor-

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<sup>1</sup> EMIL ROHDE. Ganglienzellkern und Neuroglia. Ein Kapitel über Vermehrung und Wachstum von Ganglienzellen. *Arch. f. mik. Anat.*, XLVII, 1, 1896.

tance and one which in the past neurology and psychiatry have sadly lacked. It is of course merely that generalization and integration of facts which gives to science its true stamp as science and the lack of which has so often kept these departments so far behind their sister sciences. But now all this is changed and no one can complain of the lack of generalization in neurology.

Foremost among the men in this rank Professor Wernicke places Golgi and Cajal, v. Monakow, Déjérine. The recent generalizations of Flechsig<sup>1</sup> on the association centers, or "Cogitationscentren" of the brain do not meet with equal favor. Flechsig draws a very attractive picture. At the beginning of the ninth month we find the foetus without cortical connections, practically in the condition of Goltz' decorticated dog. We watch the centripetal fibers growing up into the cortex to their respective sensation areas, beginning with the fibers of general visceral and cutaneous sensation, in the two central gyri, and followed about a month later by the olfactory fibers and still later by those of the other special senses. Between the areas thus connected there are large areas which receive no coronal fibers, but from which associational fibers develop in great numbers. These association centers are originally distinct and are only secondarily fused with each other and with the other cortical areas to form an organic whole. Their psychological importance, if Flechsig's views hold, is vast, for upon them are dependent all of the higher processes of intellect and emotion.

All this Professor Wernicke sweeps away at one stroke. Granting all of Flechsig's anatomical findings in the foetus and the child, it by no means follows that the same isolation of areas supplied by coronal fibers prevails in the adult. Indeed, he says, Flechsig's results have absolutely nothing to do with the localization of mental faculties. While it is probably true that the theoretical parts of Flechsig's work are characterized by certain excesses, yet we must believe that his discoveries have a higher significance than Professor Wernicke is willing to admit. But whatever their significance to psychology and psychiatry, there can be no doubt that Flechsig's embryological method as an instrument of anatomical research has few rivals in the field today and we predict for it a still wider application in the solution of problems in comparative morphology.

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<sup>1</sup> Those who may not be acquainted with Flechsig's original papers we would refer to the excellent digest of his researches given by Lewellyn F. Barker in the *Journal of Nerv. and Ment. Disease*, XXIV, 6, p. 329.



In the "Tagesfragen" which introduces the second number Professor Ziehen says that it must be admitted that the psychology of the psychiatry of today is several decades, often a good hundred years behind the development of psychology itself. For this modern psychology, he claims, is in large measure answerable. This is a surprising accusation, but a moment's reflection convinces one that it is not altogether unjust. We have an "experimental psychology," a psychology of measurement, which is accomplishing all that could in reason be asked of it; but where is the "physiological psychology," of which we heard so much a decade or two ago? To be sure, to cite Professor Ziehen's example, "Wundt in his *Physiological Psychology* devotes nearly 300 pages to the anatomy and physiology of the brain; but—to say nothing of numerous errors—this anatomico-physiological section is an alien in the book." "So it happens," he continues, "that in the psychiatry of today two one-sided tendencies dominate; the one is based upon brain anatomy and physiology and concerns itself at heart very little with modern psychology, the other pursues the latter and writes text-books of psychiatry in which a relation to brain anatomy and physiology is arrogantly repudiated." Then follows a plea for the application of the methods of a true physiological psychology in clinical work which will commend itself to all. And surely such counsel can come from no one with more weight than from Professor Ziehen.

C. J. H.

#### Effect of Section of the ninth Nerve upon Taste Buds.

Authors are divided regarding the question whether taste buds degenerate after the section of their nerves, and the matter has been re-investigated.<sup>1</sup> The papillæ foliatæ of the rabbit were found after section of the ninth nerve to show alterations within 30 hours. The cells of the bud did not disappear; they simply returned to the condition of the normal non-sensory epithelium, so that at the sixteenth day there was only a slight depression to mark the position of the former papilla.

Dr. Meyer calls attention to the fact that Szymonowicz has recently shown<sup>2</sup> that the Merkel tactile papillae are of epithelial origin and are developed directly under the influence of the out-growing nerve. The same is probably also true of taste buds and now we see

<sup>1</sup> DR. SEMI MEYER. *Durchschneidungsversuche am Nervus Glosso-pharyngeus*. Dissertation, Berlin, 1896; *Arch. f. mik. Anat.*, XLVIII, 1, 1896.

<sup>2</sup> *Arch. f. mik. Anat.*, XLV, p. 624.

that when the influence of the nerve is withdrawn the sensory cells return to the condition of indifferent epithelium from which they were derived. From the point of section the peripheral end of the nerve degenerates, not the central, thus again showing that the taste bud and the nerve are not organically united.

C. J. H.

#### Development of Tactile Corpuscles.<sup>1</sup>

It is interesting to compare the development of the Merkel papillae, referred to in the last notice, with a still more recent study of the development of the tactile corpuscles of the beak of the duck. The author's conclusions are as follows :

I. The tactile cells of Grandry's and Herbst's nerve-corpuscles are of connective tissue origin.

II. The differentiation of the connective tissue cells into tactile cells of Grandry's and Herbst's corpuscles takes place under the influence of the nerve fiber.

III. The sharpest distinction must be drawn between Merkel's corpuscles and Grandry's, and to include these heterogeneous structures in a single group is not admissible. The former are, as before shown, of epithelial origin, the latter of connective tissue origin. They are thus histogenetically, as well as histologically distinct.

C. J. H.

#### Nerve Termini in the Ear.<sup>2</sup>

In view of the fact that authorities are still not agreed as to the mode of termination of the auditory nerve in the ear, the author has investigated the matter again from the developmental standpoint, using complete series of trout and salmon embryos, also chick embryos. The preparations were stained by means of methylene blue *intra vitam*.

In embryos of 4.5 mm. the peripheral processes from the bipolar ganglion cells reach to the membrana propria of the undifferentiated auditory vesicle, but do not pierce the membrane to reach the epithelial cells. At 6.7 mm. the cristae acusticae have appeared and the nerve fibers penetrate them, spreading out into fan-shaped termini

<sup>1</sup> LADISLAUS SZYMONOWICZ. Ueber den Bau und die Entwicklung der Nervenendigungen im Entenschnabel. *Arch. mik. Anat.*, XLVIII, 2, 1896, pp. 329-358.

<sup>2</sup> KRAUSE, R. Die Endigungsweise des Nerv. Acusticus im Gehörorgan. *Verh. Anat. Gesellschaft*, X, 1896, pp. 165-173.

by dichotomous division between the epithelial cells. The nerve fibers do not reach more than two thirds of the way through the thickness of the epithelium. These branched termini now become more bushy and finally grow up and enclose the bases of the specific auditory cells. In older embryos (24-30 mm.) the terminal apparatus is more highly developed and is closely applied to the auditory cells, though there is not protoplasmic continuity. This stage too shows a difference between the termini of the maculae and the cristae acusticae, the former consisting of very numerous delicately branched fibrils, the latter of few, thick, short branches. The same method applied to the mammals gave essentially similar preparations.

These results with the methylene blue obviously harmonize very closely with those of Retzius, von Lenhossek and others with the chrome-silver method.

C. J. H.

### The Homologies of the Hypoglossus Nerve in Lower Vertebrates.

This old problem about which so much has been written and so little known in the past is clearly reaching the point where speculation ceases and legitimate generalization begins. Kupffer's recent extended review<sup>1</sup> has done much to clarify the matter and to indicate the gaps in our knowledge which require further investigation. The two groups most in need of further study seem to be the cyclostomes and the bony fishes. In the case of *Petromyzon*, it will be remembered that the ventral musculature of the head is innervated from the vagus, not from the first spinals, or "hypoglossus," as in most of the other lower vertebrates. Kupffer was of the opinion that this ventral musculature is not derived from the lateral musculature, as is the case with the "hypoglossus musculature" of other vertebrates; but that it is of dermal origin. Hence the difference in its mode of innervation.

The matter has been re-studied under Kupffer's direction by Dr. H. V. Neal<sup>2</sup> with quite a different result. Dr. Neal finds that this ventral musculature is developed in *Petromyxon* in exactly the same way as in the gnathostomes and is homologous throughout the vertebrate series. The *ramus recurrens vagi* of *Petromyzon* is therefore homologous with the hypoglossus of higher vertebrates, while the so-called hypoglossus of the older writers on *Petromyzon* is composed of true spinal nerves.

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<sup>1</sup> In Merkel und Bonnet's *Ergebnisse* for 1895, pp. 607-618.

<sup>2</sup> The Development of the Hypoglossus Musculature in *Petromyzon* and *Squalus*. *Anat. Anz.*, XIII, 17, 1897, pp. 441-463.

Before this homology can be universally applied, however, the aberrant teleosts must be brought into line. Here the post-hyoid portion of the ventral musculature is supplied from the first spinals in the usual way, while the pre-hyoid portion is innervated from the V+VII complex. The question now is, What are the homologies of this pre-hyoid ventral musculature (*m. geniohyoideus*) and of its innervation in the bony fishes? That it is not the *m. geniohyoideus* of the Amniota seems clear.

C. J. H.

### The Nasal Organs of the Surinam Toad.<sup>1</sup>

This paper is welcomed because it is an addition to the slowly accumulating literature upon the olfactory organs of a most instructive group of animals—the Batrachia. Here, if anywhere, are to be worked out those problems in the morphology of the olfactory organ which at present baffle the best investigators.

If the results of this investigation are to be taken as indicating a condition constant for the Aglossate group of the Anura, then the present writer's theory<sup>2</sup> as to the revolution of Jacobson's organ from a lateral to a ventral-median position seems to be supported. This view claims that the diverticle which Wiedersheim found in *Gymnophiona* (*Ichthyophis*), which has a lateral position, is the original condition of the primitive Jacobson's organ, and that in the course of the evolution of the higher types it revolved from without inward to its present position as found in *Ophidia*.

Now the similarity of conditions found in the writer's examination of the nasal organs of the Urodela (*Amblystoma*), which are probably arrested Amphibian types, and these anomalous Anura (*Pipa*) renders this view still more probable. The words of the writer whose article is here reviewed suggest a transition stage in this revolution. He says, "It [Jacobson's organ] is the most external of the cavities connected with the nasal organ and lies on a lower plane than the rest" (p. 102). *Rana* presents a further revolution: in this type Jacobson's organ "lies beneath the main nasal canal (*cavum nasale*) and extends inward as far as does any other structure connected with the olfactory region. In *Pipa*, on the other hand, it is not covered by any of the other nasal structures, and it is placed entirely

<sup>1</sup> The Nasal Organs of *Pipa Americana*, by Irving Reed Bancroft. Contributions from the Biological Laboratories of Tufts College, under the directions of J. S. Kingsley, No. XVII. (From the the Bulletin of the Essex Institute, Vol. XXVII, 1895.) The Salem Press. Salem, Mass., 1897.

<sup>2</sup> See *Jour. Compar. Neurol.*, July, 1894, p. 141.



on the external side of the whole nasal apparatus" (p. 105). The author has implicitly recognized the force of the above when he says, "It seems unnecessary to make any comparisons with the Urodeles farther than to point out that in some respects *Pipa* seems to be intermediate between these and the *Anura*, especially in the relationships of what I have called the nasal canal, which agrees well in some respects with what Seydel calls the respiratory duct. Again the position of Jacobson's organ is nearer that found in *Urodeles* than that occurring in *Rana* and *Pelobates*."<sup>1</sup>

The author says truly, "It is yet too early to say how much weight is to be placed upon the varying conditions of the olfactory organ in settling the vexed question of the inter-relationships of the *Amphibia*. Too few forms have as yet been studied to allow of any broader generalizations. Naturally one would expect to find more points of resemblance between the conditions occurring in *Pipa* and in *Rana* than between *Pipa* and the *Urodeles*, but from the foregoing account it will be seen that *Pipa* is about as widely removed in its nasal structure from the one as from the other. Certainly, if much weight is to be given these structures, naturalists are justified in the separation of the *Aglossa* from the other *Anura*."

A few typographical or orthographical errors must not confuse the reader, especially, in figure 6, the *jo* just to the right of the figure should doubtless be *jd*. Again, on page 103 the point of view (following Seydel in beginning at the choana) which was ostensibly adopted in the description is not strictly adhered to.

The statements made concerning the naso-lachrymal duct (p. 104) seem to conflict with Balfour's description of the development of this structure in *Amphibia*,<sup>2</sup> since it is figured here (fig. 5) as having already become a hollow tube although its connection is not established with the cavum nasale, while Balfour describes the latter process as preceding the former.

The author does not escape the error into which almost everyone falls more or less in reconstructing by the use of models—that of insufficient orientation. But this is somewhat alleviated by drawings of carefully selected representative sections. Too much emphasis cannot be laid upon the value of accurate modeling in morphological

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<sup>1</sup> It is instructive to compare the author's figures with the series of camera drawings of *Amblystoma* contained in the article to which reference has been made (*Jour. Compar. Neurol.*, July, 1894, Plate V).

<sup>2</sup> Balfour, F. M. *Compar. Embryol.*, II, pp. 506-507.

studies.<sup>1</sup> Its value is seen in the study before us. The value of such work is, apart from the originality of the observations, in its permanency, making practicable a comparative study of these types on the part of others.

In closing, attention is called to the need of a new nomenclature for the various parts of the olfactory organ in the different types. On the whole the paper, though brief, may be regarded as a valuable addition to the literature of the subject.

H. H. BAWDEN.

#### **A Text-book on Inebriety.<sup>2</sup>**

This well printed little book of over one hundred pages is a dispassionate and, on the whole, sensible discussion of the pathology and heredity of intemperance. The introductory remarks upon the physiology of the nervous system, while occasionally open to criticism, are well adapted to introduce a discussion of natural inheritance. The relationship between the various neurotic diseases is clearly brought out as well as the effect of these as predisposing causes of inebriety. The author drops his judicial and impartial tone for a moment to scourge the reformer who is stupid enough to think that drinking is a cause of drunkenness and to expose the absurdity of efforts to appeal to the inebriate's will power and moral feelings in the effort to control his craving, though in the end he returns to the training of these faculties as the chief means for combatting the disease. The little note of irritation is the chief defect in an otherwise quite well-balanced discussion.

He says later: "It is not extravagant to assert that the so-called moral treatment of the inebriate has been the great obstacle in the proper treatment of his case." Appeals made to a paralyzed will and to a moral sense geared out of all relation to the originative faculties can but be useless. The first step is to supply a suitable environment without impairing the self respect. The second is to supply an engrossing object which by its worthiness shall appeal to all that is best in the man's nature.

Self-control is cultivated until it becomes habitual.

Reparation of the physical damages must be left to the ordinary

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<sup>1</sup> Cf. "Wax Modeling from Microscopic Sections," by W. E. Wells, M. S., Bull. of the Scientific Laboratories of Denison University, Vol. IX, pp. 3-7.

<sup>2</sup> C. F. PALMER. Inebriety, its source, prevention, and cure. F. H. Revell Co., 1897.

natural reactions of the system. Great stress is laid upon action as a means of character building.

The importance of the subject is obvious from the great demand for the various patent remedies for drunkenness and we are glad to commend a temperate and scientific treatment of inebriety.

C. L. H.

### **The Physiology of Visual Sensation.<sup>1</sup>**

Under the above heading a series of papers, originally published in the *Zeitschrift f. Psychologie*, are in convenient form for reference.

The first paper, by the editor, concerns the function of the retinal rods.

It is found that when the eye has been adjusted to the darkness of a poorly lighted room all parts of the retina except the macula function in a peculiar way characterized by the absence of color, by a greatly increased sensitiveness to feeble light and especially to the colors with short waves in so far that it does not discern the red at all. Now if the anatomical fact that the rods are absent from the macula be coördinated with the above it is but reasonable to conclude that the peculiarities described belong to the rods of the retina.

It may then be concluded that the rods are color blind, adapted to short wave-lengths and are exceedingly adaptable. Per contra, the cones may be regarded as trichromatic organs demanding greater intensity of light. According to this theory the perception of white may be reached either by any sort of stimulation of the rods or by a definite composition of light waves affecting the cones.

The existence of these two method of producing white sensations, the author claims, affords an explanation of several vexed questions. He sums up the variations from Newton's law of color mixtures as follows:

The comparisons serving for high intensities become erroneous as the light is diminished according to the rule that the mixture which has the greater rod-valence contains a superfluity of colorless light.

Persons completely color blind may be supposed to lack the cones or the pigment appropriate to them.

In a second paper the variations due to modifications of intensity in the case of the green-blind are discussed by Kries and Nagel.

Very interesting results bearing upon the same problem were obtained by Dr. Kries in a study of the effect of brief light stimuli on the

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<sup>1</sup> *Abhandlungen zur Physiologie der Gesichtsempfindungen aus dem physiologischen Institut zu Freiburg.* Edited by J. von Kries. Part I. 1897.

retina. The divergent results obtained by different observers of "recurrent vision" (after-images from instantaneous stimuli) are ascribed to different reactions on the part of the rods and cones.

The eye adapted for daylight, as a matter of fact, produces an after-image which is complementary. Thus if the illuminated spot be blue the after-image is yellowish. On the other hand if the eye be adapted for faint illumination the after-image is white and follows without interval upon the colored one. (The apparatus used produces a spectral blue spot rotating through a small circle.) But the phenomena are not as simple as this statement might seem to indicate and cannot be referred to wholly independent reactions of the rods and cones respectively.

Dr. Kries follows with an extended and technical paper on color systems, but for this and Dr. Breuer's paper, entitled *Ueber den Einfluss des Makulapigments auf Farbengleichungen*, the reader is referred to the original.

C. L. H.

### Cajal's Recent Researches by the Golgi Method.<sup>1</sup>

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<sup>1</sup> Beitrag zum Studium der Medulla oblongata, des Kleinhirns und des Ursprungs der Gehirnnerven, by S. Ramón y Cajal; Ger. translation by Johannes Bresler; Introduction by E. Mendel. *Leipzig, Barth, 1896.*



The studies here gathered together and translated comprise, as Mendel points out in the brief Introduction, researches in the most difficult fields. In view of Cajal's previous successes along similar lines, it is with the highest expectations that we take up the work. Nor are we disappointed. To give an adequate notice of each of the sections, as outlined in the Table of Contents given above, would involve practically the translation of the entire paper; and indeed we trust that such a translation may soon be provided by some one. We can merely select at random a few of the author's suggestive results.

In the first section he re-establishes his earlier discovery (confirmed by Kölliker, Held, Van Gehuchten) that the trigeminal ganglion cells are unipolar and that the process divides T-form into peripheral and central fibers, the latter inside the medulla exhibiting the Y-shaped bifurcation so characteristic of sensory root-fibers in general. He does not confirm Van Gehuchten's account that one limb of the Y enters the so-called descending (or mesencephalic) root of the trigeminus, but regards the latter as made up exclusively of motor fibers. These ascending (cephalic) fibers of the Y are short and fine, resembling collaterals of the coarser descending fibers, though they too give off collaterals which end in the substantia gelatinosa or in the adjacent motor nucleus of the fifth nerve. Cajal thinks it improbable that any collaterals of the descending fibers (which constitute the so-called "ascending root" of the trigeminus) effect such direct reflex connections, but that they act only through the mediation of the cells of the substantia gelatinosa. He confirms in the main Kölliker's account, adding some details, of the way in which these latter cells send their processes into a secondary central trigeminal tract, which lies very near to the corresponding tract of the vagus.

If we turn now to the seventh section of this contribution and read the account of the sensory roots of the glosso-pharyngeus and vagus, the resemblance to the sensory roots of the trigeminus, as described in the first section, is striking. The trigeminal root is the bearer of general cutaneous impressions from the head. Its fibers find their terminal nucleus in the cells of the substantia gelatinosa which are distributed along the mesal aspect of the so-called ascending, or spinal, trigeminal root for its entire length and down into the cervical cord, where they become continuous with the dorsal cornu. In very much the same way the sensory roots of the ninth and tenth nerves from the viscera and mucous surfaces, including taste buds, enter the fasciculus solitarius, through the spinal portion of which they too are brought into relation with the grey matter of the

spinal cord. As the terminal nucleus of the cutaneous fibers of the trigeminal nerve is scattered along the whole course of the spinal fifth root in the substantia gelatinosa, so the terminal nucleus of the visceral fibers of the ninth and tenth nerves bears a similar relation to the more deeply lying fasciculus solitarius, with this difference that this nucleus toward its cephalic end is considerably more compacted, thus giving rise to the sensory portion of the chief vagus nucleus.

The new-born mouse is a particularly favorable subject for the demonstration of this relation. The author says, referring to the vagus and glossopharyngeal nuclei (p. 44): "There do not exist, therefore, in this animal two sensory terminal nuclei, nor two separate portions for each nerve. A single root common to both nerves proceeds without loss of fibers into the fasciculus solitarius in such a manner that between the upper, or chief, nucleus referred to and the lower, or descending, nucleus there is no distinction aside from that of position."

To complete the parallel which we have begun, we may call attention to the fact, not alluded to by Cajal, that just as the spinal trigeminal tract runs down into the dorsal horn, so the fasciculus solitarius runs down into that intermediate zone of the cord which contains Clark's column, the lateral horn and other structures which, following Gaskell, we are inclined to regard as visceral centers. To the reviewer this parallism, which has been suggested by others also, seems to be of more than passing importance, especially as it will be found to hold, he believes, throughout the entire vertebrate series. But this brings up the moot question of the homology of the fasciculus solitarius and the fasciculus communis of the Ichthyopsida, a homology, however, which he regards as established. He would even go farther and suggest that probably the transverse fibers of Cajal's "commissural nucleus" of the fasciculus solitarius of the mouse are contained in the "commissura infima Halleri" of the fishes. But these are subjects which he hopes to treat more *in extenso* shortly.

C. J. H.

#### The Nervous System of Cestodes.<sup>1</sup>

The worms were killed by immersion in v. Rath's mixture consisting of 500 cc sat. picric acid sol., 3 cc. glacial acetic acid, 5 grm. platinic chloride in 5 cc. distilled water, 2 grm. osmic acid crystals. After remaining ten hours they were cut into pieces 3 cm. long and

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<sup>1</sup> WM. L. TOWER. On the Nervous System of Cestodes. *Zool. Anz.* 508, 1896.

were placed in pyroligneous acid 6-10 hours and dehydrated in alcohols, infused with xylol and imbedded in paraffin. The nerves after this treatment are colored greyish blue, the muscles are brownish and the connective tissue remains pale.

By this means the author demonstrated the existence of transverse connections between the longitudinal nerve trunks in the proglottides. A ganglionic enlargement occurs at the point of union of the transverse with the longitudinal trunk as also in the latter between the transverse commissures.

Two kinds of cells occur in the ganglion. The commissures are connected by two pairs of longitudinal fibers and these intersections are also ganglionic. Further details are promised in the final paper.

C. L. H.

#### The Use of Corrosive Sublimate as a Fixing Medium.<sup>1</sup>

Dr. Schaper warmly recommends Zenker's solution (a mixture of bichromate of potassium, sulphate of soda and acetic acid with the mercuric chloride) on account of its superior permeability and uniform action. In this, however, as in all other methods of sublimate impregnation much embarrassment grows out of the fact that the mercuric salt tends to crystalize out within the tissue. While it is true that the salt can be removed by iodine tincture yet the injurious effects of this fluid are always apparent even if the dilute fluid is used for the shortest time possible. The injury is least when the crystals are dissolved in the sections. However, the author points out that their presence during paraffin imbedding causes serious injury to the tissues. Specimens from which the sublimate crystals were removed before imbedding proved well preserved, while a portion of the same piece not so treated but imbedded in the same way was seriously injured. The author supposes that the injury is not due to the presence of the crystals directly as the elasticity of the tissue accomodates to the foreign bodies, but when they are present during paraffin imbedding the tissues lose their elasticity and the presence of the crystals then operates to produce large cavities.

It would seem to the reviewer better to avoid a method in which such distortions are possible and to seek to prevent the crystal deposition or restrict the use of sublimate to tissues in which cytological structures are of secondary importance, Nevertheless he has secured beautiful preparations of the central nervous system with sublimate in which no crystalline deposit was formed at any time. C. L. H.

<sup>1</sup> Alfred Schaper. Zur Sublimatfixation. *Anat. Anzeiger*. XII, 17, 1897.

## LITERARY NOTICES.

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### Spino-occipital Nerves.<sup>1</sup>

The term spino-occipital nerves was applied in 1895 by Max Fürbringer to certain nerves of the selachians which have been known since the time of Stannius to occupy a more or less ambiguous position between the vagus and the first spinal nerves. The net result of the present investigation is to substantiate the last expressed opinion of Gegenbaur, that these nerves belong not with the vagus, but with the spinals, and that their relations with the vagus are in all cases secondary. This group of nerves is further subdivided into "occipital nerves," which have lost their spinal character and have become incorporated into the head, and "occipito-spinal nerves," whose emancipation from the spinal nerves is not yet complete, a distinction of degree only and not resting on any profound morphological basis. Peripherally these nerves unite with each other and with more or less of the succeeding spinal nerves to form a plexus which divides into a caudal brachial plexus for the fin and a cervical plexus for the pre-zonal somatic musculature. This plexus crosses the vagus and may be more or less intimately bound up with it, but does not form a true anastomosis with the vagus.

The importance of this region for the proper understanding of the problems of cephalogenesis can hardly be over-estimated. It is in the selachians that this series of transitional nerves is most highly developed and, accordingly, it is here that Dr. Fürbringer has done his chief work; nevertheless this exhaustive study has been supplemented by a personal examination of representatives of all of the other vertebrate classes and by a thorough mastery of the literature of all of the vertebrates. The thoroughness with which this latter work was done is indicated by the fact that the bibliography contains 560 titles and the text gives evidence that all of them were consulted.

As an illustration of the complexity of the conditions, we may cite the case of *Hexanchus*, where portions of the skull which origi-

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<sup>1</sup>Dr. Max Fürbringer. Ueber die Spino-occipitalen Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. *Festschrift f. Gegenbaur*, III, pp. 351-788, 8 plates, Leipzig, 1897.



nally were added to the paleocranium from the vertebral column (neocranium) are in the ontogeny secondarily again separated by an articulation and added to the vertebral column. Another case is that of the epibranchial and hypobranchial musculature. There is embryological evidence in both of these cases that we have derivatives of the somites here and not a visceral musculature, and the present research shows that both are innervated wholly from the cervical plexus and not from the vagus, as several previous authors have stated. But in both cases an extended comparison of many species shows that the number of myomeres does not correspond with the number of nerves which supply them nor do the myomeres correspond with the gill arches. As to the cause of this dysmetamerism, it is suggested that probably migrations of the pectoral fin constitute a disturbing factor, while the discrepancies between the muscles and their arches is due to the fact that these two systems of muscles having been derived from the somites their relation to the branchial arches is secondary throughout. In fact the existing branchial arrangements must be interpreted as the resultants of two opposing forces which strove for the mastery very early in the phylogenetic history of the vertebrates, the backward (caudal) growth of the branchial apparatus and the forward (cephalic) growth of the somites of the spinal trunk musculature.

Among the selachians there is evidence of the absorption into the head of the metameres corresponding to those of the occipital system of nerves; but the nerves themselves have not in the selachians been fused with the proper paligenetic nerves of the head (branchial nerves); on the other hand this system is always very distinct from that of the vagus. Furthermore the occipital nerves give evidence of a progressive reduction from before backward, as indicated by the fact that their number is greater in the lower members of the group (Notidanidæ) and becomes progressively less up to the higher (Rajidæ) and by the fact that they diminish in size as we pass cephalad. This reduction is correlated with that of the corresponding body segments, the sensory elements having disappeared first.

In a few cases (e. g., Notidanidæ) the last occipital nerve retains its dorsal root and ganglion in the adult; in other cases one or more dorsal roots have a transitory appearance in the embryo. The degeneration of the dorsal sensory roots of the occipital and occipito-spinal nerves is explained as due the progressive encroachment of these segments into the domain of the vagus, so that they have been replaced by the rami laterales of the X and IX nerves. The principle seems to be

that in the conflict, above referred to, between the somatic metameres, which push forward, and the branchiomeres, which push backward, the motor spinal nuclei migrate cephalad under the motor vagus nucleus, while the corresponding sensory spinal nuclei are checked in their migration by the sensory vagus nuclei and hence degenerate, their peripheral areas being supplied by the vagus.

To this principle we assent, but in its application in the present instance it seems to us that Dr. Fürbringer has perpetuated an ancient and very pernicious morphological error. That is, he regards the sensory rami of the spinal nerves and the ramus lateralis of the vagus as equivalent structures, while the fact is that recent research has abundantly shown that these nerves belong to entirely distinct categories of sensory nerves, having no relation to each other either centrally or peripherally, and to regard them as equivalent or capable of replacing each other is bad morphology, as well as bad physiology. General cutaneous nerves, such as the dorsal rami of the spinal nerves, cannot be either functionally or morphologically replaced by special cutaneous nerves, such as the rami laterales of the X and IX nerves, which belong to the acustico-lateral system. Nor is such an unnatural substitution necessary, for we know that in the other Ichthyopsida, and presumably in the Selachii, the vagus contains other fibers which do belong to the general cutaneous component. These are derived from the spinal V tract and are distributed with the supratemporal rami of X and IX. They may accompany lateralis fibers but can be distinguished from them. A survey of the existing literature leaves no doubt in the mind of the reviewer that similar relations will be found to prevail in the selachians. It is therefore the rami cutanei dorsales of the X and IX nerves and not their rami laterales that have replaced the dorsal rami of the spino-occipital.

Again in the final comparison between the true cranial and the spinal nerves (p. 570), Dr. Fürbringer states that with reference to the homology (in the broad view) of the sensory roots of the cranial and spinal nerves there is scarcely any controversy. This is a very rash statement in view of the recent work on the components of the cranial nerves (Pollard, Strong, Cole, Kingsbury, Herrick), for the evidence is rapidly accumulating that the special cutaneous components (acustico-lateral and communis systems) are neomorphs in the head and that the general cutaneous (spinal V) system is the only representative in the head of the cutaneous nerves of the trunk.

The principle involved in this criticism has a profound and far-reaching application. The comparisons instituted in some of our

ablest researches in morphology and especially in embryology between the cranial and the spinal nerves are futile because their authors have attempted to homologize disparate structures. The lateral line nerves especially must be rigidly excluded from all such comparisons, for this is the component whose independence has been most conclusively demonstrated.

Dr. Fürbringer has traced the connection between the caudal, or ascending, motor root of the vagus and the trapezius muscle, and thus verifies the supposition that this root represents the accessorius Willisii. He controverts the view of Stöhr, Wiedersheim and others that this nerve is a descendant of the spinal nerves, and argues that the vago-accessorius is a unit and a primordial cranial nerve. Its central relations certainly favor this view, yet peripherally there are several points of difficulty, even if we were to accept, as Dr. Fürbringer does, Gegenbaur's theory of the origin of fins from gill arches. The comparative anatomy of both the m. trapezius and the ventral musculature between the pectoral arch and the gill arches (cleido-branchialis, Fürbringer; Paryngo-clavicularis, Vetter) is by no means satisfactorily settled. For example, in the bony fishes Fürbringer regards the m. cleido-branchialis as innervated from the occipito-spinal nerves and the m. trapezius from the vagus. But McMurrich describes both muscles in *Amiurus* as innervated from the spinals, Vetter gives instances in which the trapezius is innervated by the spinals and the cleido branchialis by the vagus, and the present writer can vouch for one case where both muscles are supplied by the vagus.

In some of these cases it is difficult, if not impossible, to decide these questions with the scalpel and we must resort either to electrical stimulation of fresh material or to reconstruction from serial sections. It is not impossible that several of these cases may occur among the bony fishes. Such a fact, if it be a fact, would suggest a series of most interesting morphological problems.

The reduction from before backward, which was observed in the spino-occipital nerves of the Ichthyopsida, continues progressively as we ascend the taxonomic series, so that the general rule may be laid down that among the adults of almost every class of vertebrates the more primitive forms are characterized by more, the higher forms by fewer, of the spino-occipital nerves. The embryology in most cases where it is known recapitulates more or less completely the steps in this reduction. The higher mammals have lost from five to six of the first spinal metameres, as compared with the lower selachians.

The motive for this forward movement of the somatic metameres



the author finds in the loss of the more cephalic myotomes through progressive reduction of the gills and hence of the epibranchial and hypobranchial somatic musculature. The lower selachians may perhaps be regarded as marking more nearly than any other existing types that stage of the phylogenesis at which the tendency to extend the gills caudad was finally mastered by the thereafter dominant tendency in the opposite direction, i. e. reduction of the gills, the assimilation of spinal metameres into the head and the loss of the first members of the spinal series. Beginning with the selachians, then, we distinguish, using Gegenbaur's terms, the neocranium from the paleocranium; at the caudal limit of the latter stand the X and XI neuromeres. In the primitive selachians and amphibians certain of the spinal nerves have become fully incorporated into the head (the occipital nerves of Fürbringer) and these neocranial segments comprise the protometameres of Sagemehl. In all other vertebrates the process of further assimilation is taking place under our eyes and the result is a series of transitional nerves ("occipito-spinal nerves" of Fürbringer), whose segments comprise the auximetameres of Sagemehl. But especial stress is laid upon the fact that in spite of these fusions, throughout the Gnathostomata the neocranial elements can always be sharply distinguished from the paleocranial, i. e. the IX+X+XI nerve complex never contains spinal elements.

Regarding the criteria for fixing the boundary between the brain and spinal cord and between the head and the trunk, a very radical position is taken. It follows from the above exposition that in the nervous system this limit will lie between the X + XI and the occipital nerves and that so far from being a plane surface, it will zigzag between the nuclei of these nerves. Thus in *Hexanchus* it runs ventrally far cephalad to include with the spinal cord the nuclei of the occipital nerves, but also farcaudad to include the whole of the XI nucleus with the brain. This is extended also to the longitudinal tracts, so that the pyramids, e. g., are ranked with the head throughout their length. Among the other tissues, the hypoglossus musculature is relegated to the trunk, while the head includes the ramus lateralis vagi, the ramus recurrens trigemini [facialis], the visceral ramus of the vagus and the *organs which these nerves supply*. While this procedure has more to commend it than the arbitrary limits of His and Huxley, and while some of the most extreme examples of the termination of nerves in metameres apparently far removed from the one in which they originate (e. g., the ramus lateralis vagi and the hypoglossus) can be explained by the cenogenetic migration of the organs



which they supply ; yet it will not do at present to affirm that a nerve can never supply an organ which has originated out of its own metamer. In other words, the innervation of an organ cannot in the present state of our knowledge be taken as an infallible guide to its metamerism. It is, of course, possible that subsequent research may remove the apparent exceptions. Fürbringer's attitude on the question is explained by his unswerving devotion to the neuromuscular theory, to which he devotes a section in the appendix.

At the conclusion of the summary of the first and second sections, which deal with the Selachii and the higher vertebrates respectively, a few genealogical considerations are adduced. The arrangements of these organs in the vertebrates support in general the accepted taxonomy. Among the Selachii the Notidanidæ are the most primitive, the bony fishes connect with the ganoids through amioid forms, the Dipnoi occupy a quite isolated position, the Amphibia connect with the Crossopterygia, and the Urodela and Gymnophiona are more primitive than the Anura. The Myxinoidæ are far separated from the Petromyzontidæ and given a class by themselves.

The third section contains an exhaustive study of the first spinal nerves of the cyclostomes and *Amphioxus*, which leads to the conclusion that the third or fourth spinal nerve of *Petromyzon* is homologous with the first of the Notidanidæ, while the myxinoids possess three spinal nerves which lie cephalad of the first of *Petromyzon*. This latter condition is regarded as a primitive one, and it follows that the lowest selachians have already lost five or six of their spinal nerves.

The leading motives of this third section are suggested by two questions of fundamental importance :

(1) The general homology of cranial and spinal nerves and in particular, What is the relation between the visceromotor nerves of the head (V, VII, IX and X + XI) and the somatic motor nerves of the head (III, IV and VI) and between these nerves and the motor nerves of the trunk ?

(2) Are the most cephalic spinal nerves of cyclostomes, which appear to have been lost in all higher forms, perhaps represented in the III, IV (?) and VI nerves ; and, if so, were these nerves originally spinal nerves which have secondarily migrated into the head, or were they from the first pre-vagal (paleocranial) nerves ?

Under the first head, the author's attempt to dismiss the sensory nerves with the off-hand remark that the general homology of cranial and spinal sensory nerves is scarcely controverted, we have already

had occasion to criticize. But the treatment of the motor nerves, which were the chief subjects of the author's own research, is masterly throughout.

Regarding the composition of the typical spinal nerves, he comes to stand very nearly upon the ground of van Wijhe and Gaskell. The ventral root is composed of somatic motor and visceral motor fibers; the dorsal root, of somatic sensory, visceral sensory and visceral motor. The latter arise from the lateral cells of Lenhossék and Cajal. Now in the cranial nerves the somatic motor nerves are represented by the eye-muscle nerves only, while the motor roots of the other cranial nerves belong exclusively to the visceral systems, their nuclei being equivalent to the lateral nuclei of the spinal cord. The V, VII, IX and X cranial nerves therefore represent the dorsal roots only of the spinal nerves and contain no somatic motor elements. They are therefore homodynamous with each other, but not exactly with the spinal nerves. These conclusions, to be sure, are not new; but the evidence from phylogeny brought forth in support of them by Dr. Fürbringer is of a new order and may be said to clinch the demonstration. These are conclusions, moreover, to which the reviewer has in the main also been led, and indeed had already formulated for the press, from his own studies of the bony fishes.

The second question propounded above is given a very thorough critical treatment, but receives by no means so satisfactory an answer as the first one. The reason for this is not far to seek, for neither the embryology nor the adult anatomy of the critical forms has been sufficiently thoroughly worked up. Dr. Fürbringer inclines to the opinion that the eye-muscle nerves are paleocranial, i. e., that they are indigenous to the head and have not migrated into it from the spinal region.

Taken as a whole this splendid research is an abundant justification of its author's contention that the thorough knowledge of the structure of an organ, and especially of its comparative anatomy, is an essential pre-requisite for the proper interpretation of embryological data concerning its ontogeny. It is a work which no writer on the deeper problems of the vertebrate head can afford to ignore.

We add a full translation of the final tables, giving the author's views of the metamerism of the head. It should be noted that he regards the data of the first table as far more in need of confirmation than those of the second table.

# A. Metamerism of the cerebral (paleocranial) nerves.

<i>Myomeres.</i>	<i>Ventral nerves.</i> <i>Vent. (myal) roots.</i>	<i>Visceral arches.</i>	<i>Visceral muscles.</i>	<i>Lateral (septal) roots.</i> <i>Dorsal Nerves.</i> <i>Dorsal (septal) roots.</i>
?	?	?	?	?
1. myomere pt. red. ( <i>A</i> ). Lost ( <i>M</i> ). Obl. inf., rect. sup. and int. ( <i>P</i> ). Obl. inf., rect. sup., int. and inf., intrabul- bar m. ( <i>Gn</i> ).	1. ventral n. lost ( <i>A</i> ). Lost ( <i>M</i> ). Oculomotorius ( <i>P</i> , <i>Gn</i> ).	Trabecular arch ? ( <i>P</i> ). 1. First labial carti- lage arch, pt. red. ( <i>Gn</i> ).	Lost ( <i>A</i> , <i>M</i> , <i>P</i> , <i>Gn</i> ).	1. dorsal (?) n. ( <i>A</i> ). N. thalamicus ? n. apicis ? ( <i>Gn</i> ).
2. myomere ( <i>A</i> ). Lost ( <i>M</i> ). Obl. sup. of opposite side of body ( <i>P</i> , <i>Gn</i> ).	2. (1.) ventral n. ( <i>A</i> ). Lost ( <i>M</i> ). Trochlearis ( <i>P</i> , <i>Gn</i> ).	Palatine arch ? ( <i>P</i> ). 2. Second labial car- lage arch ( <i>Gn</i> ).	Sphinct. oris ? ( <i>A</i> ). M. of tentacles and nasal tubes ( <i>M</i> ). Lost ( <i>P</i> , <i>Gn</i> ).	Mot. part of 2d. dors. n ? ( <i>A</i> ). Mot. part of r. oph. prof. V ( <i>M</i> ). Lost ( <i>P</i> , <i>Gn</i> ).
3. myomere ( <i>A</i> ). Lost ( <i>M</i> ). Rect. inf. and ext. ( <i>P</i> ). Rect. ext. and retr. bulbi etc. ( <i>Gn</i> ).	3. (2.) ventral n. ( <i>A</i> ). Lost ( <i>M</i> ). Abducens ( <i>P</i> , <i>Gn</i> ).	3. Mandibular arch ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	Sphinct. oris ( <i>A</i> ). Most m. of mandib. arch, hyoid bone & soft pal. ( <i>M</i> ). M. of ant. cartilages hyoid, tongue & soft palate ( <i>P</i> ). Constr. m. of mandib. arch ( <i>Gn</i> ).	Motor part of 3 dors. n. ( <i>A</i> ). Motor part of r. man. V ( <i>M</i> , <i>P</i> , <i>Gn</i> ). Sens. part of rest of V. ( <i>M</i> , <i>P</i> , <i>Gn</i> ).

4. myomere ( <i>A</i> ). Lost ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	4. (3.) ventral n. ( <i>A</i> ). Lost ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	4. Hyoid arch ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	Sph. oris et veli ( <i>A</i> ). Some m. of hyoid arch, part of constr. pharyng. ( <i>M</i> ). Pharynx m. in region of hyoid arch ( <i>P</i> ). Constr. of hyoid arch ( <i>Gn</i> ).	Motor part of 4 dors n. ( <i>A</i> ). Motor part of r. hyoid. VII ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	Sens. part of 4 dors. n. ( <i>A</i> ). Sens. part (incl. acusticus) of VII ( <i>M</i> , <i>P</i> , <i>Gn</i> ).
5. — 10. myomeres ( <i>A</i> ). Lost ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	5. — 10. (4.-9.) ven. n. ( <i>A</i> ). Lost ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	5. First gill arch ( <i>M</i> , <i>P</i> , <i>Gn</i> ).	Sph. oris et veli ( <i>A</i> ). Part of constr. phar. ( <i>M</i> ). Constr. branch. of 1st gill bar ( <i>P</i> ). M. of 1st gill bar ( <i>Gn</i> ).	Motor part of 5 dors. n. ( <i>A</i> ). Motor part of beginning of r. phar. vagi ( <i>M</i> ). Motor part of r. post-trem. IX ( <i>P</i> , <i>Gn</i> ).	Sens. part of 5 dors. n. ( <i>A</i> ). Sens. part of beginning of r. phar. vagi ( <i>M</i> ). Sens. part of IX n. ( <i>P</i> , <i>Gn</i> ).
11. to cir. 27. myomeres ( <i>A</i> ). Unknown how many of them were originally formed in <i>M</i> , <i>P</i> and in ancestors of <i>M</i> , <i>P</i> and <i>Gn</i> ; in <i>M</i> possibly one and <i>Gn</i> all lost.	11. to cir. 27. (10. to 26.) ven. n. ( <i>A</i> ). Unknown how many of them were formed in <i>M</i> , <i>P</i> and in ancestors of <i>M</i> , <i>P</i> and <i>Gn</i> ; in <i>M</i> possibly one and <i>Gn</i> all lost.	6-11. Numerous hypermetameric gill arches ( <i>A</i> ). Perhaps the existing branchiomeres ( <i>M</i> ). 2d. to 7th. gill arches ( <i>P</i> , <i>Gn</i> ).	Sph. veli for 6, Sph. atrii for 7-11 ( <i>A</i> ). Constr. phar. poss. also con. branch. of some gills ( <i>M</i> ). Constr. branch. of 2-7 gill arches, ant. part of m. trapezius ( <i>P</i> , <i>Gn</i> ). Sph. Atrii ( <i>A</i> ). Constr. branch. of an unknown no. of gills, constr. card., m. of gut ( <i>M</i> ). Intestinal m. ( <i>P</i> ). Intest. m., trapezius, interscap. ( <i>Gn</i> ).	Motor part of 6-11 dors. n. ( <i>A</i> ). Mot. pt. r. phar. & some rr. branch. vagi ( <i>M</i> ). Motor part of rr. branch. post-trem. 1-6 vagi ( <i>P</i> , <i>Gn</i> ).	Sens. part of 6-11 dors. n. ( <i>A</i> ). Sens. part of r. phar. & some rr. br. vagi ( <i>M</i> ). Sens. part of vagus, esp. of the rr. branch. ( <i>P</i> , <i>Gn</i> ).
		12 to cir. 28. Numerous hyper-metameric gill arches ( <i>A</i> ). Unknown which & how many arches formed in ancestors of <i>M</i> , <i>P</i> , and <i>Gn</i> ; several preserved in <i>M</i> ; all lost in <i>P</i> ; in <i>Gn</i> only those in the girdles of the limbs preserved.		Motor part of 12 to cir. 28 dors. n. ( <i>A</i> ). Motor part of an unknown no. of segments of X, possibly also one behind ( <i>M</i> ). R. intest. vagi ( <i>P</i> ). R. intest., trap. and interscap. vagi ( <i>Gn</i> ).	Sens. part of 12 to cir. 28 dors. n. ( <i>A</i> ). Sens. part of an unknown no. of segments of X, possibly also one behind ( <i>M</i> ). Sens. part of r. intest. of vagus ( <i>P</i> , <i>Gn</i> ).



# B. Metamerism of the spinal and neocranial nerves.

<i>Muscles supplied by ventral roots (myomeres).</i>	<i>Ventral nerves. Ventral (myot) roots.</i>	<i>Visceral muscles supplied by lateral roots.</i>	<i>Lateral (septal) roots.</i>	<i>Dorsal Nerves. Dorsal (septal) roots.</i>	
Myomere (A). 2 first myomeres? (M). Lost (P, Gn).	Vent. sp. n. (A). Vent. sp.-occ. n. s (M). Lost (P, Gn).	Visc. muscles (A).	Visc.-mot. part of dors. spin. n. (A). Lost (M, P, Gn).	Sens. part of dors. spin. n. (A). Dors. sp.-occ. n. s (M). Lost (M, P, Gn).	1. (s).
1. (s).					
Myomere (A). 3d. myomere (M). 1st. pre-brachial myomere (P). Lost (P, Gn.)	Vent. sp. n. (A). Vent. sp.-occ. n. t (M, P). Lost (Gn).	Visc. muscles (A, M? P?).	Visc.-mot. part of dors. spin. n. (A). Visc.-mot. part of dors. sp.-occ. n. t? (M, P). Lost (Gn).	Sens. part of dors. sp. n. (A). Sens. part of dors. sp.-occ. n. t (M, P). Lost (Gn).	2. (t).
2. (t).					
Myomere (A). 4th. myomere (M). 2d. pre-brachial myomere (P). Lost (Gn).	Vent. sp. n. (A). Vent. sp. n. u (M). Vent. sp.-occ. n. u (P). Lost (Gn).	Visc. muscles (A, M, P?).	Visc.-mot. part of dors. sp. n. (A). Visc.-mot. part of dors. sp. n. u? (M). Visc.-mot. part of dors. sp.-occ. n. u? (P). Lost (Gn).	Sens. part of dors. sp. n. (A). Sens. part of dors. sp. n. u (M). Sens. part of dors. sp.-occ. n. u (P). Lost (Gn).	3. (u).
3. (u).					

4. (v).	Myomere (A). 5th. myomere (M). 3d. myomere (P). Sbs, begin. of lat. trunk m. (Not.) Lost (other Gn).	Ventral sp. n. (A, M). Ventr. sp. n. v (P). Ventr. occ. n. v (Not.) Lost (other Gn).	Visc. muscles (A, M, P).	Visc.-mot. part of dors. sp. n. v (A, M, P). Lost (Gn).	Sens. part of dors. sp. n. v (A, M, P). Lost (Gn).	4. (v).
5. (w).	Myomere (A). 6th. myomere (M). 4th. myomere (P). Sbs., begin. of lat. trunk m. (Not., some pentam. sharks). Lost (other Gn).	Ventral sp. n. (A, M, P). Ventral occ. n. w (Not., some pentam. sharks). Lost (other Gn).	Visc. muscles (A, M, P).	Visc.-mot. part of dors. sp. n. w (A, M, P). Lost (Gn).	Sens. part of dors. sp. n. w (A, M, P). Lost (Gn).	5. (w).
6. (x).	Myomere (A). 7th. myomere (M). 5th. myomere (P). Sbs., lb. 1, hyp.?, lat. trunk m. (many sharks, Acipenser ind., Dipnoi ind.). Lost (other Gn).	Ventral. sp. n. (A, M, P). Ventr. occ., n. x (many sharks, Acipenser ind., Dipnoi ind.). Lost (other Gn).	Visc. muscles (A, M, P).	Visc.-mot. part of dors. sp. n. x (A, M, P). Lost (Gn).	Sens. part of dors. sp. n. x (A, M, P). Lost (Gn).	6. (x).

# B. Metamerism of the spinal and neocranial nerves.—Continued.

<i>Muscles supplied by ventral roots (myomeres).</i>	<i>Ventral nerves.</i> <i>Ventral (myal) roots.</i>	<i>Visceral muscles supplied by lateral roots.</i>	<i>Dorsal Nerves.</i> <i>Lateral (septal) roots.</i>	<i>Dorsal (septal) roots.</i>	
Myomere ( <i>A</i> ). 8th. myomere ( <i>M</i> ). 6th. myomere ( <i>P</i> ). Sbs. 1b., hyp., lat. trunk m. (most sharks, Holocceph., many ganoids, Dipnoi). Lost (other <i>Gn</i> ).	Vent. sp. n. ( <i>A, M, P</i> ). Vent. occ. n. <i>y</i> (most sharks, Holocceph., many ganoids, Dipnoi). Lost (other <i>Gn</i> ).	Visc. muscles ( <i>A, M, P</i> ).	Visc.-mot. part of dors. sp. n. <i>y</i> ( <i>A, M, P</i> ). Lost ( <i>Gn</i> ).	Sens. part of dors. sp. n. <i>y</i> ( <i>A, M, P</i> ). Lost ( <i>Gn</i> ).	7. ( <i>y</i> ).
Myomere ( <i>A</i> ). 9th. myomere ( <i>M</i> ). 7th. myomere ( <i>P</i> ). Sbs. 1b., hyp., lat. trunk m. (most Sel., Holoc., Gan., Dip., Cryptobranchus ind., Echidna?). Lost (other <i>Gn</i> ).	Vent. sp. n. ( <i>A, M, P</i> ). Vent. occ. n. <i>z</i> (most Sel., Holoc., Gan., Dip., Cryptobr. ind., Echidna?). Lost (other <i>Gn</i> ).	Visc. muscles ( <i>A, M, P</i> , Not.?).	Visc.-mot. part of dors. sp. n. <i>z</i> ( <i>A, M, P</i> ). Visc.-mot. part of dors. occ. n. <i>z</i> ? (Not., Ceratodus ind.). Lost (other <i>Gn</i> ).	Sens. part of dors. sp. n. <i>z</i> ( <i>A, M, P</i> ). Sens. part of dors. occ. n. <i>z</i> (Not., Ceratodus ind.). Lost (other <i>Gn</i> ).	8. ( <i>z</i> ).
Myomere ( <i>A</i> ). 10th. myomere ( <i>M</i> ). 8th. myomere ( <i>P</i> ). Ib.?, hyp., lat. trunk m. (most Anamnia, many Amniota). Lost (most Amniota, here the tongue m.).	Vent. sp. n. ( <i>A, M, P</i> ). Vent. sp. n. <i>i</i> (most Sel., most Amphibia). Vent. occ.-sp. n. <i>a</i> (some sharks, Holoc., Gan., Dip., many Amniota (hypoglossus)).	Visc. muscles ( <i>A, M, P</i> , some sharks, most ganoids, Dipnoi).	Visc.-mot. part of dors. sp. n. <i>i</i> ( <i>A, M, P</i> , some sharks). Visc.-mot. part of dors. sp.-occ. n. <i>a</i> (most Gan., Dip.). Lost (other <i>Gn</i> ).	Sens. part of dors. sp. n. <i>i</i> ( <i>A, M, P</i> , some sharks). Sens. part of dors. sp.-occ. n. <i>a</i> (most Gan., Dip.). Lost (other <i>Gn</i> ).	9. ( <i>i, a</i> ).

10. (2, b).	Myomere ( <i>A</i> ). 11th. myomere ( <i>M</i> ). 9th. myomere ( <i>P</i> ). Hyp., lat. trunk m. (Anamnia, most Amniota, here the tongue muscles).	Vent. sp. n. ( <i>A, M, P</i> ). Vent. sp. n. 2 (Sel., Polypt., Amphibia). Vent. occ.-sp. n. $\delta$ (Holo., most Gan., Telos., Dip., most Amniota (hypoglossus)).	Visc. muscles ( <i>A, M, P</i> , most Anamnia, some Mammalia).	Visc.-mot. part of dors. sp. n. 2 ( <i>A, M, P</i> , most sharks, many Amphibia). Visc.-mot. part of dors. sp.-occ. n. $\delta$ (most Gan., Tel., Dip., some Mam.). Lost (other <i>Gn</i> ).	Sens. part of dors. sp. n. 2 ( <i>A, M, P</i> , most sharks, Polypt., many Amph.). Sens part of dors. sp.-occ. n. $\delta$ (most Gan., some Tel., Dip., some Mam.). Lost (other <i>Gn</i> ).	10. (2, b).
11. (3, c).	Myomere ( <i>A</i> ). 12th. myomere ( <i>M</i> ). 10th. myomere ( <i>P</i> ). Hyp., lat. trunk m. ( <i>Gn</i> ), in Amniota tongue m.).	Vent. sp., n. ( <i>A, M, P</i> ). Vent. sp. n. 3 (Sel., Polypt., Dipn., Amph.). Vent. occ.-sp. n. $\epsilon$ (Holo., most Gan., Tel., Ceratodus ind., Amniota (hypoglossus)).	Visc. muscles ( <i>A, M, P</i> , Anamnia, several Mammalia).	Visc.-mot. part of dors. sp. n. 3 ( <i>A, M, P</i> , Sel., Polypt., Dip., Amph.). Visc.-mot. part of dors. sp.-occ. n. $\epsilon$ (most Gan., most Tel., sev. Mam.). Lost (Holoceph., most Amniota).	Sens. part of dors. sp. n. 3 ( <i>A, M, P</i> , Sel., Polypt., Dip., Amph.). Sens. part of dors. sp.-occ. n. $\epsilon$ (most Gan., most Tel., sev. Mam.). Lost (Holoceph., most Amniota).	11. (3, c).
12. (4).	Myomere ( <i>A</i> ). 13th. myomere ( <i>M</i> ). 11th. myomere ( <i>P</i> ). Hyp., lat. trunk m. ( <i>Gn</i> ).	Vent. sp. n. ( <i>A</i> ). Vent. sp. n. 4 (Sel., Polypt., Dip., Amph.). Vent. sp. n. 4 = 1 (Holo., most Gan., Tel., Dip., Amniota).	Visc. muscles ( <i>A, M, P</i> , Anamnia, some Sauropsida, most Mammalia.).	Visc.-mot. part of dors. sp. n. 4 ( <i>A, M, P</i> , most <i>Gn</i> ). Lost (most Saurops., some Mam.).	Sens. part of dors. sp. n. 4 ( <i>A, M, P</i> , most <i>Gn</i> ). Lost (most Sauropsida, some Mam.).	12. (4).
Follow- ing	Following myomeres.	Following ventral nerves.	Following visceral musculature.	Following lateral nerves.	Following dorsal nerves.	



## EXPLANATION OF THE TABLES.

The occipital nerves are designated from before backwards by the last letters of the alphabet, *s* to *z*; the occipito-spinal nerves from before backwards, by the first letters of the alphabet, *a* to *c*; the spinal nerves are serially numbered, beginning with the first occipito-spinal.

*Abbreviations.*

( <i>A</i> ).—Amphioxus.	( <i>P</i> ).—Petromyzontidæ.
begin.—beginning.	pal.—palate.
esp.—especially.	pentam.—pentamerous.
( <i>Gn</i> ).—Gnathostomata.	Polypt.—Polypterus.
hyp.—hypobranchial musculature.	poss.—possibly.
Ib.—m. interbasilis.	pt.—part, partially.
ind.—individuals.	red.—reduced.
lat.—lateral.	sbs.—subspinal epibranchial somatic musculature.
( <i>M</i> ).—Myxinoidæ.	sev.—several.
m.—muscle [ <i>s</i> ].	sp.—spinal.
n.—nerve [ <i>s</i> ].	sph.—sphinctor.
Not.—Notidanidæ.	sp.-occ.—spino-occipital.
occ.-sp.—occipito-spinal.	

Other abbreviations are self-explanatory.

C. J. H.

**Recent Progress in Neurology.<sup>1</sup>**

The increase in quantity and quality of neurological publications is very well illustrated by the present number of Edinger's report in Schmidt's *Jahrbücher*. The great works of Kölliker and Dejerine indicate how fully the detailed results of the past decade have been digested. The influence of Edinger's new edition of his lectures will be even more potent in clarifying the vision of investigators.

The perplexities of an undigested nomenclature are hardly lessened by the results of the German Nomenclature Commission, as may be gathered from Professor Wilder's article and the results of the questionnaire in our present number. The introduction of formalin into neurological technique and Bethé's modification of the methylene blue intra-vitam method are perhaps the most important technical improvements, though the neuroglia stain of Weigert should also be mentioned. It has been experimentally shown that functioning causes a rapid development of tissue and this fact, long since postulated, now rests on observed data.

<sup>1</sup> EDINGER AND WALLENBERG. Bericht über die Leistungen auf dem Gebiete der Hirnanatomie in den Jahren 1895 und 1896.

Descriptive anatomy offers less of interest than histology which, especially in the case of the cerebellum, has taken long strides. The *Bericht* has attained proportional extent, the present number occupying 67 closely printed pages and yet every reader will wish that some subject had been treated more fully.

C. L. H.

### The Peripheral Zone of the Cortex.<sup>1</sup>

It has been obvious to all who have carefully studied the cortex that far too little attention has been given to its outermost zone. For one thing it seems hardly to have dawned upon histologists that the embryological stage when the cortex has a double proliferating zone of cells at the periphery is of primary significance in understanding later transformations. This fact is equally ignored or misunderstood by embryologists. We are glad, therefore, that attention is now being directed to this field.

Dr. Lewis recognizes two types of connective tissue structures, (a) small cells (6-9 micra) with a proportionally large nucleus enveloped by scanty protoplasm scattered irregularly along the course of blood-vessels, adjacent to nerve cells and in the brain substance; (b) larger cells (13 micra) of flask-like contour and abundant protoplasm and having two kinds of processes; first, such as are extremely radiating and, second, coarse processes invariably attached to blood-vessels by a sucker-like foot. The last mentioned cells stain very feebly except in degenerate (paralytic) states. The vascular branch of these (Deiters) cells is not subdivided.

The author derives these from the primitive epithelial lining and he believes that all "spider cells" pass through the three stages characterized by, first, embryonic moniliform fibers, pertaining to epithelial elements, second, true spider-cell features of vascular attachments, third, fine stellate fibers of neuroglia. (It may be remarked in passing that in lower vertebrates the sustentive tissue can be traced very easily to derivatives of the epithelial layer of spongioblasts.) The transition from Andriezen's true neuroglia or stellate cells to the spider cells the author claims to have clearly demonstrated.

The tangential fiber belt is very rich in fibers which are not only parallel to the surface but at times dip into deeper levels. Some of the fibers can be traced long distances and give off collaterals at frequent intervals to terminate in arborizations about pyramid cells.

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<sup>1</sup> W. BEVAN LEWIS. The Structure of the First or Outermost Layer of the Cerebral Cortex. *Edinburgh Med. Journ.*, June, 1897.

A few nerve cells may be detected, but not enough, as the author believes, to afford origin for all the axis cylinders of the tangential zone. The latter is, he suggests, the locus for extensive association by contiguity or continuity. Respecting the question as to which of these methods prevails he insists upon conservatism in view of conflicting testimony.

In the second layer Dr. Lewis believes that sensory cells predominate and that it is possible to differentiate distinct types of the sensory cell corresponding to different cortical regions. He therefore agrees with Golgi and the present writer rather than Cajal.

He adds, "Our conception, therefore, of the peripheral zone resolves itself into that of an enormous field of the cortex, in which sensory units are brought into close contiguity with the terminal dendrites of the motor pyramidal cells, and that, though sensory-motor arrangements are to be found at most levels of the cortex, this field is *facile princeps* that whereon the transference of sensory currents to motor energy is realized."

The reader is referred to the original for details and interesting illustrations.

C. L. H.

#### A Modified Sublimate Method.<sup>1</sup>

A method which, judging from the results obtained by Dr. Lewis, surpasses in some respects all previous modifications of the Golgi process is described by its author as follows:

"When a section prepared by Golgi's *rapid* method is subjected to the action of a drop or two of liquor potassæ on a slide, the removal of the diffuse red coloration is at once observed, whilst the nerve-cells and *all* their processes remain deeply stained on a clear background. The connective elements also participate in this coloration, and are seen to fine effect. The potash should be removed as rapidly as possible, by gently inclining the slide and allowing a little water from a pipette to flow over the section, but no longer than is absolutely necessary for its complete removal. At this stage the whole tissue swells out and becomes greatly expanded, as it does in the perfectly fresh state; and this expansion, as before stated, is so great that we find subsequently the dendrites are split across in fine fractures at more or less regular intervals along their course. This splitting of the dendrons is of interest, as it appears to indicate how truly the silver-

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<sup>1</sup> W. BEVAN LEWIS. On a Modified Sublimate Method for the Delination of Nervous Tissue. *Edinburgh Med. Journal*, Aug. 1897.

chrome coloration is a *genuine* staining of the interior of the nerve-process; for along the gap betwixt two separated fragments of the process, we often observe an extremely delicate margination, as though of a more extensile, sheath-like investment, from which the stained contents have retracted and split across. Should the section itself be unduly thick, the subsequent process tends occasionally to cause also slight conchoidal fractures near the margin of the section as it dries; this, however, can be avoided by employing thin sections only. It is useless to dehydrate by alcohol, and mount in balsam, since the shrinking entailed in the former *after the action* of potash is extreme, and ruins the preparation. Such sections must be dried on the slide and mounted in xylol balsam. The dendrites and neurons are well seen in these preparations, the fine bulbous projections along the former being uninjured, whilst the whole cerebral tissue is unfolded.

“If, now, in lieu of using specimens prepared by the quick silver-chromate, we harden in the sublimate fluid of Cox, we entirely obviate the disadvantages of the above procedure; the sections are *not expanded* by the potash; they undergo to a still greater degree the differentiation of staining seen in silver-chrome preparations; they can be mounted, after dehydration by spirit and clearing in clove oil, in balsam; and undergo no undue shrinking, and present no injuries to the delicate nerve processes. Cox’s fluid is a modification of the sublimate method of Golgi, and is highly spoken of by Cajal.<sup>1</sup> Brain cortex requires immersion in this fluid for two to three months ere it is sufficiently stained for our purpose. The pieces are then well washed in alcohol for half an hour to remove superfluous sublimate; the cut sections are cleared in clove oil, and mounted in balsam. One great advantage of this solution is the absence of much diffuse staining, as shown by the silver-chrome method, the background being a pale yellow hue.

“Now, if one of these sections be treated similarly by liquor potassæ, an immediate darkening of the tissue elements is observed by the naked eye, and tissue which, prior to this treatment, remained unstained, now starts out in bold relief; so that sections prepared

<sup>1</sup> See his remarks in “*Les Nouvelles Idées sur la Structure du Système Nerveux*,” p. 185. Cox’s fluid consists of—

5 per cent. solution of bichromate of potash	20 parts.
5 “ “ bichloride of mercury	20 “
5 “ “ chromate of potash	16 “
Distilled water	30 to 40 “



simply by the Cox method are greatly enhanced in value by the potash treatment. The finest details of structure which have hitherto been revealed by the mercury and silver-chrome methods are beautifully brought out by this means. Nor do I know any process which can compete with it for wealth of structure and beauty of delineation. We sacrifice, it is true, the rapidity of other methods of preparation, but this is greatly counterbalanced by the certainty of results which appear to be ensured by Cox's fluid, and the far greater beauty of the sections. Sublimate preparations were at one time proverbially uncertain in results; the potash treatment of sections, prepared as above described, is open to no such criticism. It was stated in the earlier note that liquor ammoniæ is ruinous to the silver-chrome preparation (chromate of silver being soluble in excess of ammonia); this is not so in the sublimate preparations. Solutions of potash, soda, or ammonia may be used, though I give preference to the former."

#### **Darwin and after Darwin, Vol. III.<sup>1</sup>**

This concluding volume, like the second one of the same series, was left unfinished at the time of the author's death. The most important parts of the work were, however, already in type and we may rest assured that these pages accurately represent his most mature thoughts upon the questions discussed. This is undoubtedly the most important volume of the three, for it is here that Mr. Romanes' most valuable direct contributions to the theory of evolution are found. The dominant note is indicated by the sub-title, *Isolation*, and by this is meant simply the prevention of intercrossing, Weismann's *Amixia*. The barriers are of various kinds, geographical, physiological, etc., and the isolation may be *Indiscriminate*, i. e., without reference to the resemblances of the separated individuals to one another, or *Discriminate*, i. e., the separation of a group of individuals on the basis of certain distinguishing characters which they have in common. *Indiscriminate isolation* has no special evolutionary significance, except in so far as it tends to pass into the discriminate type. But *discriminate isolation* is shown to be of the most fundamental importance; indeed according to Romanes' view it is more fundamental than natural selection itself in that the latter is but a mode of isolation in which the isolation is with reference to superiority or 'fitness' and is effected by

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<sup>1</sup> GEORGE JOHN ROMANES. *Darwin and after Darwin. III. Post-Darwinian Questions. Isolation and Physiological Selection.* Edited by Prof. C. Lloyd Morgan. Chicago: The Open Court Publishing Co., 1897. Cloth, \$1.00.

the death of the excluded individuals. Natural selection differs from most of the other forms of isolation in that, acting alone, it is not capable of producing *divergent* or *polytypic* evolution, for the only way in which isolation of any form can cause such evolution is by partitioning a given group into two or more groups, each of which is able to survive as thus separated from the other, and so carry on the evolution in divergent lines. But the distinguishing peculiarity of natural selection, considered as a form of isolation, is that it effects the isolation *by killing off all the individuals which it fails to isolate*.

These points are developed succinctly and with convincing force. Perhaps the strongest line of evidence adduced is the fact that they were elaborated quite independently by another naturalist. Indeed the remarkable resemblance between the views of Mr. Romanes and those of Mr. Gulick, developed almost simultaneously on the opposite side of the earth, reminds one forcibly of the dramatic way in which the doctrine of natural selection was simultaneously published by Darwin and Wallace.

C. J. H.

### Theories Of Upright Vision.<sup>1</sup>

The question why we perceive objects in their actual position in spite of the fact that the retinal image is inverted seems doubtless to a dynamic psychologist, a very naive one, due to a very superficial conception of the process of perception. Nevertheless it is a problem which actually gives a great deal of trouble to experienced thinkers. Two theories have been invented to explain why the image must be inverted to produce the percept of the natural position and both imply that this inversion is essential to the proper upright vision. The first theory is that the sense of position is derived from the motions of the eye balls in bringing the image of the object into the fovea. "Upper" or "lower" mean, accordingly, those directions which require an upward or downward motion of the eye to bring the objects into the field of clearest vision. The second theory is that the retina has a

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<sup>1</sup>GEORGE M. STRATTON. Some Preliminary Experiments on Vision without Inversion of the Retinal Image. *Psych. Rev.* III, 6.

JAMES H. HYSLOP. Upright Vision. *Psych. Rev.* IV, 2.

GEORGE M. STRATTON. Upright Vision and the Retinal Image. *Psych. Rev.* IV, 2.

GEORGE M. STRATTON. Vision without Inversion of the Retinal Image. *Ibid.* IV, 4, 5.

C. H. JUDD. Some Facts of Binocular Vision. *Ibid.* IV, 4.

A. CAMERON. The Imagery of One Early Made Blind. *Ibid.* IV, 4.

mysterious power of projecting the perceived object in the direction from which the incident rays come. It is noticed by Dr. Hyslop that this statement is too simple, the rays do not reach the retina in parallel lines but in converging cones so that he finds it necessary to so modify the theory as expressed by LeConte as to take the axial direction of each pencil the direction in which the outward projection is performed and this becomes practically a perpendicular to the surface. (The reviewer is unable to see how this assumption of perpendicularity assists, by analogy with the process of outward projection in the skin, as Hyslop seems to hold.)

In the first of the above theories it appears that the muscle contractions mysteriously afford a knowledge of direction which the purely visual process is incompetent to produce. We have, in fact, even in this case, to find the origin of the sense of position in the assimilating of various experiences from diverse senses and it is not apparent why the reverse notions of the muscles would not serve the purpose in hand as well. In the second theory the power of outward projection is the very thing to be explained and it does not appear that the analogy from the tactile sphere really explains anything, as the eccentric projection is there a result of experience and if the organs were differently constructed it is reasonable to suppose that essentially the same tactile impressions would be formed by a different process. It is plain that if one could subject himself for a sufficiently long time to an experience in which all images are caused to fall upon the retina in the upright position the result would be to permanently invert the percepts if either of the theories mentioned were true, while if our ideas of position and direction are formed as a product of experience, it might be possible to readjust the percepts so that the new position would cease to appear abnormal or inverted. To determine which of these suppositions would prove correct was the purpose of Dr. Stratton's painstaking experiments. This was done by binding upon the eye an erecting system of lenses which caused the retinal image to be upright. At all times when not wearing the apparatus the eyes were carefully blindfolded. The compass of the field of vision was 45 degrees. Objects at first, of course, all seemed inverted but they were lacking in the predicates of reality for which memory images from previous experience continued to be the criterion. Things were seen in one way and thought of in a different way. Soon the vivid connection of tactual and visual perceptions began to overcome the effect of previous visual vestiges and hands and feet began to seem to be in the place where vision reported them, but objects out of the field of

view were conceived of in the old position. As time went on the feeling of uprightness gradually returned, especially when dynamic vestiges were called into action, as in performing rapid motions. Although the duration of the experiment was obviously too short to overcome a life-time of ordinary experience, yet the experiment conclusively proves that the inverted position of the retinal image but is a product of experience. We are unable to see how any of Dr. Hyslop's arguments or illustrations impair the force of these conclusions. The paper by Mr. Judd cannot be summarized here but the discussion of some phases of binocular parallax tends to confirm the association and motor sensation theory rather than the reverse.

C. L. H.

### Variation of Acuteness of Sensation with Age.<sup>1</sup>

The author has investigated the reaction to moderate and painful stimuli in the case of individuals of different ages and from various classes of society. The faradic current was used and the voltage employed was used to estimate the excitement. Details of the method are not given; but the results in the case of general sensibility, as well as painful sensations, show that the sensitiveness in both is smaller in early years and increases until maturity, only to diminish again in age. Mental discipline serves to enhance this sensitiveness. These facts are not to be neglected in pedagogy and forensic psychiatry.

C. L. H.

### The Mammalian Rhinencephalon.<sup>2</sup>

Twelve animals were operated on and examined by the Marchi method in order to determine if possible the connections of the bulbus and especially to determine whether commissural fibers exist in the olfactory tracts. Recognizing the fila olfactoria as the primary projection system, the search was, of course, for the elements of the systems of higher order. After separation of the bulb from the brain it was found that the lateral tract of coarse fibers degenerates throughout the whole course to the bulb and lobus pyriformis. These are the neurites of the mitral cells (specific olfactory epithelium cells).

If a part of the bulbus is also injured the degeneration involves fibers of the third order, i. e., those arising in the bulbus. Part of

<sup>1</sup> OTTOLENGHI, S. Das Gefühl und das Alter. *Zeitschrift f. Psychol. und Phys. d. Sinnesorgane*, IX, 5, 6.

<sup>2</sup> S. LOEWENTHAL. Ueber das Riechhirn der Säugethiere. *Festschrift z. LXIX Versam. Deutsch. Naturf. u. Aerzte*.



these fibers pass parallel to the tractus lateralis and end in the pyriform lobe though there are fibers connecting the two tracts. Considerable degeneration in the cornu Ammonis (alveus and fascia dentata) indicates a connection between the olfactory lobe and the hippocampus via a tract in the septum. [The author's evidence is not quite clear here.] Other fibers degenerate in the cephalic part of the pre-commissure. The author agrees with Köl liker that a part of the pre-commissural fibers end in arborizations about the mitral cells of the tuber, but he finds that a considerable portion consists of fibers originating in the lobe of one side and terminating in the tuber of the other. In this connection it is noted that operations upon embryos (Gudden's method) cause a degeneration of the peripheral part of a tract and an atrophy of the central part, while by Marchi's method only the former is observed. It is therefore possible that the callosum and other commissures do not connect homologous parts as once supposed. It would seem to the reviewer that in order to understand the coordination of bilateral functions it is necessary to suppose the connection to be indirect and that this is to be theoretically expected, for the reaction of one centrifugal element upon another similar element on the opposite would only be possible through a suitable centripetal element.

A small degenerate portion is found in the pyriform lobe of the uninjured side. The source has not been identified, but the fibers are supposed to cross in the caudal part of the precommissure. A decussation of fibers to the hippocampus was also noticed.

C. L. H.

### Epilepsy.<sup>1</sup>

This volume of 420 pages is composed of lectures delivered this year by Dr. Jules Voisin at the Salpêtrière. The work is a general treatise on Epilepsy, particularly in its clinical aspects. After having depicted the epileptic in all his physical and mental modalities, the author treats of the diagnosis, prognosis, pathology, and treatment. A chapter is devoted to the necessary precautionary measures in order to protect the epileptic in society and to protect society against him, and another to the medico-legal aspects.

That feature which gives to the work a special appropriateness at this time and which will doubtless attract the most general interest is

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<sup>1</sup> DR. JULES VOISIN. *L'Epilepsie*. Paris, 1897. Felix Alcan, éditeur. 6 fr.

the clinical work prosecuted by the author or under his direction upon post-paroxysmal albuminaria, urinary toxicity and the condition of the blood of epileptics.

C. J. H.

### **Organic Selection.<sup>1</sup>**

Professor Baldwin's argument is interesting as an illustration of an attempt to escape from the doctrine of inheritance of acquired characters through the mediation of "organic selection." Acquired characters or individual adaptations, while not directly inherited, are influential in determining the course of evolution indirectly; for such modifications keep certain animals alive and in this way screen the variations which they represent from the action of natural selection and so allow new variations in the same directions to arise in the next and following generations; while variations in other directions are not thus kept alive and so are lost. "The species will therefore make progress in the same directions as those first marked out by the acquired modifications and will gradually 'pick up' by congenital variation the same characters which were at first only individually acquired. The result will be the same, as to these characters, as if they had been directly inherited, and the appearance of such heredity in these cases, at least, will be fully explained."

The reviewer is unable to see how the process described and illustrated differs from the inheritance of acquired characters or, if these be excluded, how the species "picks up" the characters. The illustration chosen of the young fowls kept alive by the fact that the mother teaches them to drink until the drink instinct is developed would, if substantiated, be a clear case of inheritance of acquired habit. Although we do not perceive the force of the author's claim for organic selection we are grateful for the emphasis laid on intelligence as a factor of evolution.

C. L. H.

### **The Discrimination Threshold for Distances on the Skin.<sup>2</sup>**

This extensive paper should at least serve a good purpose in checking much wasteful effort in this line due to uncritical methods. In the first place it makes very plain that much which has been attributed to the results of practice grows out of suggestion and that the subject who is ignorant of the nature and results of the experiment becomes

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<sup>1</sup> BALDWIN, J. MARK. *Determinate Evolution*. Princeton Contr. to Psych.

<sup>2</sup> TAWNEY. *Ueber die Wahrnehmung zweier Punkte mittelst des Tastsinnes*, Princeton Contr. to Psychology, II, 1, 1897.

less rather than more accurate in his estimates as a result of loss of attention. It seems to the reviewer that the use of blunt divider points serves to invalidate this class of experiments. It was found that the unsophisticated subject often reported several impacts where there was really but one. May this not be due to the fact that the pressure of a blunt point affects several tactile corpuscles and to the further fact that there is actually communication between corpuscles in the skin providing for irradiation (cf. Dogiel)? The proper method of experiment might be the use of a leather shield laid upon the skin and having small perforations through which the needles or points could be passed, the pressure of the close-fitting shield being so great as to prohibit attention to the slight pressure and flexion due to the points. In this way also a proper orientation is possible.

C. L. H.

#### **Influence of Mental Effort on Blood Pressure.<sup>1</sup>**

The only satisfactory study of the variations of blood pressure in man due to thought is that of Kiesow (*Arch. ital. de Biol.* 1895). In the author's attempts to extend these observations Mosso's sphygmomanometer was used. It was noted that the amplitude of pulse vibration varies independently of the blood pressure. This fact greatly complicates the method, making it necessary to supplement the record of pulse tracing by a record of the actual variation at the most favorable counter pressure. The curve of pressures of the state of rest has a greater amplitude than that of intellectual work. A diminution of pulse due to vascular constriction may be inferred. On the other hand the pulse is more resistant to higher pressures, hence there is greater vascular pressure during mental effort.

C. L. H.

#### **A Cortical Centre for Spelling.<sup>2</sup>**

From a study of six cases of aphasia, details of which cannot be given here, Dr. Eskridge arrives at the conclusion that an area at the foot of the second frontal convolution presides over the memories of the arrangement of the letters in words. The letters may be formed perfectly but they are confused and jumbled together so as to be unintelligible. The areas involved were localized by operation which in some cases produced a degree of relief.

C. L. H.

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<sup>1</sup> BINET AND VASCHIDE: *Psych. Rev.* IV, 1, Jan. 1897.

<sup>2</sup> J. T. Eskridge. *Speech Defect as a Localizing Symptom.* *Medical News*, Sept. 19th, 1897.

**Gray's Anatomy<sup>1</sup>**

In giving to the public a new edition of the well known Anatomy of Henry Gray, the American publishers undertook a task for which the time was thoroughly ripe. In the three branches of the subject on which, particularly, revision has been bestowed—Histology, and Visceral and Nervous Anatomy—the progress of our knowledge has been pronounced, and characteristic of the scientific methods newly invoked by human anatomists. The section on the brain is written by Dr Gallaudet, the general editor. That Dr. Gallaudet has succeeded to a certain extent in modernizing Gray is undeniable. In the place of crude illustrations and vague descriptions, he has substituted the more careful work of German investigators, reproducing Mihalkovics for the embryological, for the regional and sectional anatomy, Schwalbe, Gegenbaur and Henle. Yet it is as certain that these “new” descriptions are behind the times by at least fifteen years. Not alone original articles, but text-books, such as Edinger, v. Gehuchten, even Quain, which embody the result of more recent research, have been entirely neglected. The description of the internal course of the fifth nerve may be quoted by way of example. Of the so-called Ascending Root, it is said that “its fibres may take origin from the cells of the tubercle of Rolando, but this is considered doubtful. Passing upwards this root enters the pons, and contributes most of the fibres of the regular sensory root of the nerves.” Doubtful, indeed! Further on: “each root [of the fifth] is seen to divide just before reaching its nucleus into two bundles, the smaller of which, in each case, goes to the nucleus, while the other takes a distinct course, differing for the two roots, thus: the non-nuclear division of the motor root passes upward as a distinct bundle through the dorsal part of the pons and into the mid-brain, where its fibers terminate in a group of large nerve cells situated in the gray matter on the side of the aqueduct of Sylvius. This is the so-called descending root of the fifth nerve. The ‘non-nuclear’ division of the sensory root is the so-called ascending root.” Descriptions such as this, which for the modern students have hardly even an historical value, might be multiplied almost ad libitum. In the paragraphs on the microscopic anatomy of the cortex, it is sad to find that preference has been given over Cajal to the useless but elaborate descriptions of the pre-Golgi epoch.

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<sup>1</sup> Anatomy, Descriptive and Surgical, by Henry Gray. A new edition, thoroughly revised by American authorities, from the thirteenth English edition, edited by T. Pickering Pick. Lea Brothers and Co., Philadelphia and New York. 1896.



The prestige of Gray's text-book is so great, and its use in our medical schools so widely spread, that it has seemed advisable to give a timely warning against the misconceptions under which the editor labors.

R. WEIL.

### The Conducting Element of the Nervous System<sup>1</sup>

The means by which impulses are conveyed to and from the cells, has been and still remains one of the most fundamental problems of neurology, and any contribution dealing with this or allied problems must be of great interest, whatever its bearing on generally accepted views. Dr. Apathy's monograph appearing from the Naples Zoological Station is certainly one of the most significant of recent publications bearing on the relations of the nervous elements to each other and to the periphery. It is an article of 254 pages, illustrated by 9 plates, and its subject and scope are well expressed in the title. It is the final (partial) communication of the results of ten years' investigation. The views entertained, which are quite at variance with those generally accepted at the present time, were presented in 1887 in much the same form as in the present monograph.<sup>2</sup>

The order in which the results appear is admirable; an introduction presents a summarized statement of the conclusions, together with a terse discussion of their bearing and significance. The second and principal portion is occupied by the original observations, followed in turn by a discussion of the special methods employed.

The conducting portion (axis-cylinder) of nerve fibers, our author finds is made up of fibrillæ which he terms "primitive" or "neuro-fibrillæ," these again being formed of "elementary" fibrillæ (Elementar-fibrillen). In accordance with their relation to these conducting fibrils, two classes of nervous elements are recognized, which are termed "nerve" cells and "ganglion" cells. The nerve cells are the producers of the neuro-fibrillæ and are to be regarded as analogous to muscle cells, developing conducting substance as muscle cells form contractile substance. From these cells the fibrillæ grow centrally into the ganglion cells, while peripherally their distribution is to muscle, sense cells etc. Within the ganglion cells the neurofibrillæ break up into a mesh-work uniting again to leave the ganglion cell in a process. The further course of the neurofibril might be back immediately to the

<sup>1</sup> APATHY, STEPHAN. Das leitende Element des Nervensystems und seine topographischen Beziehungen zu den Zellen. Erste Mittheilung. *Mitth. aus d. Zoolog. Stat. Neap.* Bd. XII, 4, pp. 495-748. Pl. 23-32.

<sup>2</sup> *Biol. Centralbl.*, Vol. IX., 1889, p. 608.

periphery and a simple reflex mechanism be formed with but a single impulse generator in its course; or the fibril might go from ganglion cell to ganglion cell until at last it reached the muscle, closing the circuit. Throughout its entire course the fibril might be the product of a single nerve cell. Ganglion cells would, then, be, as it were, merely interpolated in the conducting tract as batteries. Ganglion cells produce that which is to be conducted, the impulse; the nerve cells, that which will conduct, the fibrillæ. Such, in brief, is the rather elaborate scheme of the relations of nervous elements which Dr. Apathy presents as the result of his investigations.

The forms upon which his results were obtained comprise some six genera of the Hirudinea and *Lumbricus*, and for comparison were investigated Mollusca (*Unio*, *Anodonta*), Crustacea (*Astacus*), and Vertebrata (*Triton*, *Lophius* and *Lepus*). The annelids were found most servicable because of the size and isolation of the fibrillæ and the ease with which they submitted themselves to the reagents employed, as well as the location and construction of the nervous system. At the other extreme, the vertebrate tissue was most unfavorable. In all of the forms, however, the neurofibrillæ were demonstrated, although in the present article attention is largely confined to the annelids.

These results are, it is almost needless to state, unique. The author recognizes fully the wide divergence of his results from the generally accepted views of nerve development and the relation of nerve cells to each other as based largely on the investigations of His and by means of the chrome-silver impregnation methods. Indeed, a protest is expressed against the ease with which generalizations based on vertebrates alone are made to include lower forms that are simpler and more important from a theoretical point of view. The protest seems to have real application and force. Among others, the results of Kupffer on *Amphioxus* and Platt on *Necturus* show us that the development of the nerve fiber as an outgrowth of the ganglion cell cannot be accepted as proven even for all vertebrates. Evidence from forms below Reptilia is still needed. A doubt, also, has been expressed by some and probably exists in the minds of others, whether the relation of nerve cell to nerve cell is that of contiguity only and not a continuity of their processes, and if the impregnation methods have not just failed to reveal to us the whole truth. These are secondary considerations which help to make the views of the author more plausible. It is so purely a question of evidence that any discussion at this time is fruitless. The comparison with vertebrates is unsatisfactory; however there is promised a second communication

upon this subject, which is to comprise a discussion of the conditions in Mollusca and Vertebrata, together with a critical consideration of the views of others. This may be awaited with interest and with it the present article can be more satisfactorily judged.

The original observations in support of the views entertained occupy the bulk of the paper and are presented in five sections dealing with (a) the neurofibrillæ, (b) the nerve and neuroliga cells of the Hirudinea, (c) the ganglion cells (his usage), (d) anastomoses between ganglion cells in the central and peripheral systems, (e) relation of the neurofibrillæ to the cells at the peripheral end of the fiber.

In conclusion a discussion of the methods employed is given. The chrome-silver impregnation methods were found altogether inadequate; the methylene blue methods, gold chloride methods and a special hæmatoxylin stain were those employed to stain the fibrillæ. In the manner of using all three, however, special modifications were found necessary which are set forth in detail.

B. F. KINGSBURY.

### Cortical Lesions after Thyroid Poisoning.<sup>1</sup>

Experiments were made with thyroid feeding of insane patients and of mice and Guinea-pigs. In the case of the lower animals the feeding was continued until death ensued. The autopsy showed congestion of all the viscera, but no demonstrable lesions other than this. The cortical cells seemed perfectly normal, with none of the varicose and atrophied dendrites found in poisoning by alcohol etc. Dr. Berkley concludes :

“It is obvious from these results that the death of the various animals was induced by an entirely different kind of intoxication than that causing the lesions of the nerve elements in ricin and alcohol toxæmias, and it is therefore a poison that does not induce degenerative alterations in the sheaths of the arteries, and the consequent disturbance of the nutritive supply, followed by pronounced changes in the neurons, dependent to a certain degree upon the intensity of the vascular lesions; but acts upon the general system in an entirely different manner, and is essentially more subtle in its effects upon the nerve tissues, corresponding more to the action of a group of chemical poisons that leave no trace of their effect after death upon the

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<sup>1</sup> HENRY J. BERKLEY. Studies on the Lesions Induced by the Action of Certain Poisons on the Cortical Nerve Cell. Study VII. Poisoning with Preparations of the Thyroid Gland. *Bull. Johns Hopkins Hospital*, VIII, 76, July, 1897.

nerve cell, but during life inducing symptoms directly referable to the central nervous system. The tissue metabolism induced by the action of these poisons upon the nerve cell we can only at present conjecture."

C. J. H.

### **The Psychology of Sufficient Reason.<sup>1</sup>**

The problem of selective accommodation, according to the author, is: How is it possible that from motor reactions, based entirely on their utility to the organism, judgments of 'worth' arise which are not of the nature of reactions upon the environment but give rise to the abstract concept of truth?

The more developed the psychical organism the greater the degree of selection manifested in the will acts. There is then a substitution of imaginative processes for the external reaction and this imaginative process is that which gives the sense of reality to our thinking.

The sufficiency of the motive as well as that of the psychological ground of a judgment lies in each case in the affective side of the imaginative complex. The paper is interesting as an attempt to trace dynamic influence into a difficult sphere.

C. L. H.

### **Double Conduction in the Central Nervous System.**

Dr C. S. Sherrington in the Proceedings of the Roy. Society (Vol LXI, No. 373, 1897) publishes some very interesting experiments which he interprets as showing that the fibers of the dorsal columns of the spinal cord may conduct centrifugally, as well as centripetally. For example, movements of the hind limb and the perineum were obtained by excitation of the funiculus gracilis after transection of the medulla oblongata above the point of excitation, and these the author interprets as due to the transmission of the stimulus down the dorsal columns and through collaterals to motor nerve units. This of course is directly opposed to the law of the "dynamic polarization of neurons" of Cajal and van Gehuchten, which asserts that the neurite is always cellifugal, the dendrite cellipetal. The evidence does not, however, seem perfectly clear that in Dr. Sherrington's cases it is the same nerve fibers that perform the conduction in both directions<sup>2</sup> and the whole subject, which is of great theoretical importance, offers an inviting field for further study.

C. J. H.

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<sup>1</sup> URBAN. Princeton Contrib. to Psych. Vol. II, No. 2, Sept. 1897.

<sup>2</sup> Compare also M. Allen Starr in the Journal of Nervous and Mental Disease, Vol. XXIV, No. 8, p. 452, who argues that all columns of the spinal cord contain fibers passing in both directions.



**Cortical Nerve Termini.<sup>1</sup>**

Dr. Berkley controverts the belief, widely current among students of Golgi preparations, that the mere interlacing of dendritic processes of nerve fibers is sufficient to ensure nervous conduction by contiguity. He argues that the finest ramifications of these processes, as well as the cell bodies, are enclosed in an insulating membrane and that the terminal bulbs of the gemulæ, or thorns, constitute the only avenue of approach not thus protected. He figures collaterals from the psychical cells which, winding among the dendrites, seldom show any definite endings until the mid-portion of the layer of small pyramidal cells is reached. There they split up into a number of very fine branches, and eventually give off at frequent intervals exceedingly short collaterals, which ordinarily come off from the parent stem only on the side of the nearest dendritic processes. These terminate in little bulbs which are closely adjusted against the bulbous tips of the gemmules of the dendritic process and it is between these terminal bulbs that the discharge passes from one nerve unit to another, either by continuity or contiguity, probably the latter. The transmission of impressions from external sources to the central cell and from local cell to local cell is not accomplished by a diffusion of the excitation through the whole cortex, nor diffusely through the neuropilem; but at single points, perfectly definite in their distribution, these points being situated only at the extremities of the nerve fiber twigs, viz. the bulbous endings.

C. J. H.

**Variations in the Brachial and Lumbo-Sacral Plexus.<sup>2</sup>**

Variations in the position of the pelvic girdle in vertebrates have frequently been described. In one of the best known instances, *Necturus*, Mr. Waite has undertaken the investigation of the lumbo-sacral plexus to determine whether the nerves composing it exhibit variations which can be correlated with those of the vertebræ. Thirty dissections were made and the variations of the nerves are shown to follow approximately but not exactly those of the vertebræ. Comparison with the brachial plexus shows that in case of displacement caudad

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<sup>1</sup> HENRY J. BERKLEY. The Intra-cerebral Nerve-fiber Terminal Apparatus, and Modes of Transmission of Nervous Impulses. *The Johns Hopkins Hospital Reports*, Vol. VI, 1897.

<sup>2</sup> F. C. WAITE. Variations in the Brachial and Lumbo-Sacral Plexi of *Necturus maculosus* Rafinesque. *Bull. Mus. Comp. Zoology, Harvard College*, XXXI, 4, Nov., 1897.

there has been no vertebra intercalated between the two plexuses, and the author concludes from evidence which we cannot here review that neither intercalation nor excalation of vertebræ nor slipping of the sacrum has taken place, but that the abnormal position of the girdle represents the development of a new girdle at a new point, or rather, as he states elsewhere and which is not exactly the same thing, the girdle may be called forth at primarily different distances (measured in segments) from the cranium under the stimulus of limb formation. In general, nervous and skeletal parts are not directly correlated, but only through their common relation to the muscular system, as suggested by Fürbringer and Eisler.

The author's generalizations are carefully made and are of considerable importance to the study of meristic variation, though the data are too meager to permit a very far reaching application at present. We may note in passing that the word plexus is of the fourth declension and we can find no good authority, either Latin or English, for the plural form plexi, as used in this paper.

C. J. H.

### The Neuroglia.<sup>1</sup>

Edinger has characterized Weigert's great monograph as revolutionary and one of the most important books of its year. This is doubtless true, and that too independently of the ultimate truth or error of that author's conclusions, which must be regarded as in part at least still *sub judice*; for it marks an era of special activity evoked, as usual, by advances in technique. Some of the evidences of this activity appear in the papers cited below, which were partly called out

<sup>1</sup> WEIGERT, CARL. Beiträge zur Kenntniss der normalen menschlichen Neuroglia. *Abh. d. Senckenberg'schen Naturf. Ges. in Frankfurt a-M.*, XIX, 1, 1895.

MALLORY, FRANK B. *Centralbl. f. allg. Pathol. u. path. Anatomie*, VI, p. 753, 1895.

EURICH, F. W. Studies on the Neuroglia. *Brain*, XX, 77-78, 1897, p. 114. The Human Neuroglia—Glioma and Neuroglioma. Editorial in *The Jour. Am. Med. Assoc.*, XXIX, 23, 4 Dec., 1897.

TAYLOR, EDWARD WYLLYS. A Contribution to the Study of Human Neuroglia. *Jour. Experim. Med.*, II, 6, Nov., 1897.

THOMAS, H. M. and HAMILTON, ALICE. The Clinical Course and Pathological Histology of a case of Neuro-glioma of the Brain. *Ibid.*

ROBERTSON, W. F. The Normal Histology and Pathology of the Neuroglia (in Relation Specially to Mental Diseases). *Jour. of Mental Science*, XLIII, 147, Oct., 1897.

by Weigert's work, partly independent of it. That the familiar pictures of the supporting cells with their wealth of dendritic processes given by the Golgi method afford at best an imperfect knowledge of their structure is plain; but the step to the radical position of Weigert that neuroglia cells and fibers are in the human adult quite separate and distinct is a long one. In this connection Dr. Robertson's results with his methyl violet method merit especially careful study. He claims that the adult neuroglia fibers are highly differentiated protoplasmic products, but that they normally remain in anatomical and physiological union with the cell body from whose protoplasm they were differentiated.

C. J. H.

#### **The Histological Basis of the Neuron Theory.**

Under the above title Dr. David I. Wolfstein contributes to the *Cincinnati Lancet-Clinic* of Dec. 11, 1897 an excellent historical and critical account of the labors of the leading European workers with the Golgi method, accompanied by 35 photographs of original preparations. The photographs have evidently suffered somewhat in the reproduction; nevertheless they and the accompanying text will be found very useful, especially to that large class of actively practicing physicians who cannot find time to consult the original memoirs.

In the same line mention should be made of the very admirable series of papers in the *New York Medical Journal* (Vol LXV, No 20, seqq.) by Dr. Lewell's F. Barker, entitled, The Anatomy and Physiology of the Nervous System and its Constituent Neurones, as revealed by Recent Investigations, which covers somewhat similar ground, with numerous illustrations copied from the original sources.

C. J. H.

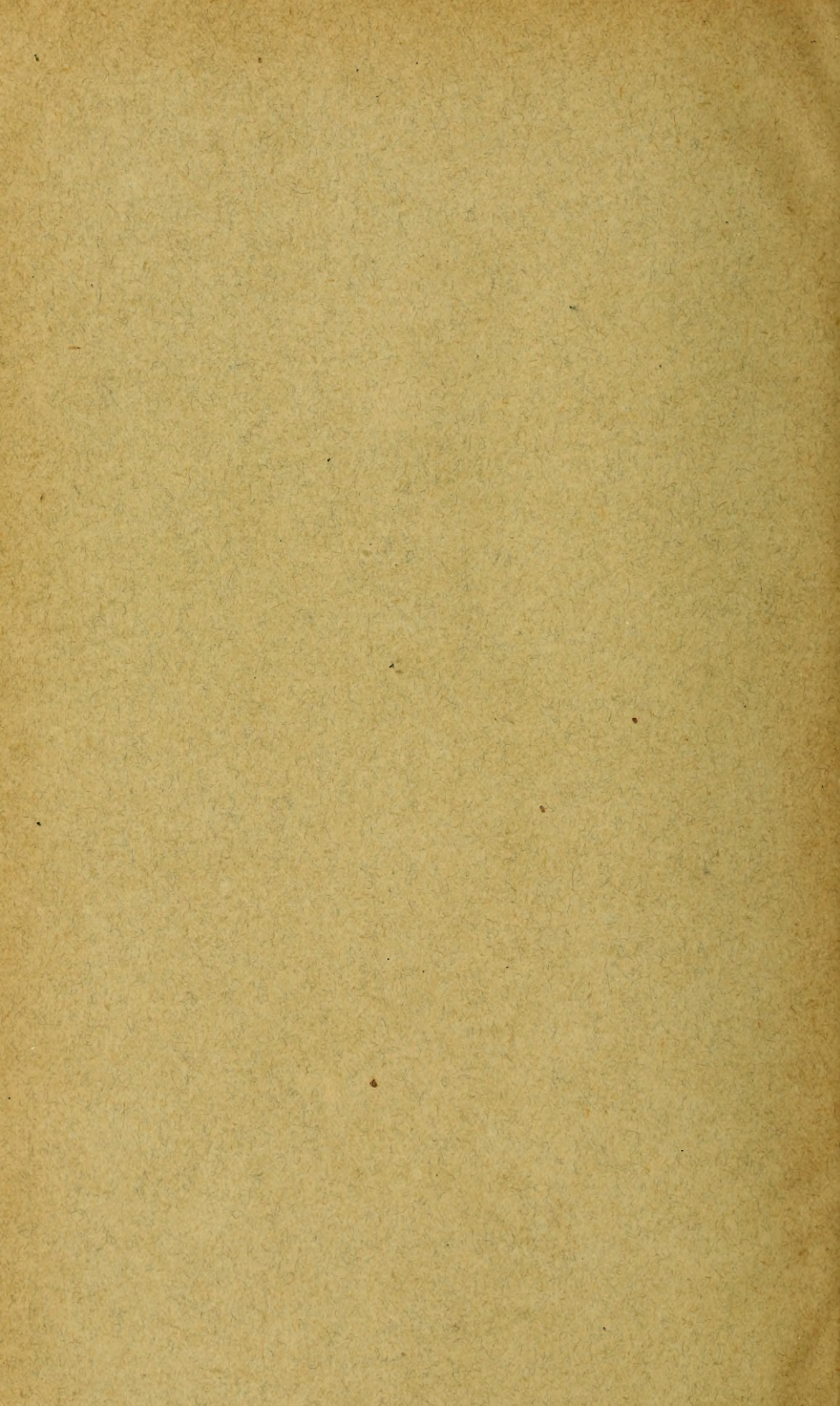












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